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Fossil Estherians and allied fossils

By

Teiichi KOBAYASHI

PREFACE

Since JONES described *Estheria middendorfii* from Transbaikalia in 1862, abundant and extensive distribution of fossil Estherians has been gradually brought to light in Eastern Asia by YOKOYAMA (1894), MANSUY (1912), OZAWA and WATANABE (1923), CHERNYSHEV (1930), CHI (1931) and others. While Estherians and their allies developed in Europe more in the Neo-Palaeozoic than in the Mesozoic era, it was just the reverse in Asia, indicating phyletic rejuvenescence.

Less is known of Mesozoic stratigraphy of this continent than Palaeozoic, because the Mesozoic formations are mostly non-marine sediments deposited in separate basins. Repeated crustal movements disturbed their sequences and facies, and leading fossils are difficult to find therein.

As an aid in correlating these non-marine formations on the continent I took up Estherians to see if there is any index fossil. Since 1941 I carried on a study of the collections from various formations and localities in Japan, Korea and Manchuria, jointly with my students and assistants. The results were published from time to time in separate papers by KOBAYASHI and HUZITA (1942–43), TANI (1943), KOBAYASHI and KIDO (1943, 47), KOBAYASHI (1952) and KOBAYASHI and KUSUMI (1953). As a result the Mesozoic Estherians can now be classified into four groups,—the Daido, Jehol, Kyöngsang and Sungari groups.

While these descriptive studies were going on, I looked into the literature on the subject to learn more about Conchostracan palaeontology. Since JONES' monograph on fossil *Estheriae* was published in 1862, a tremendous number of species has been described from all over the world, although I have not heard of any from Greenland and Antarctica. In fact more than 250 *forms*, or species plus varieties and formae, of Estherians without radial ornaments and some 50 of Leaians

and Estheriellians with radial carinae or ribs are known at present. They are distributed in over 30 genera inclusive of subgenera.

In 1946 RAYMOND undertook a comprehensive revision of fossil Conchostraca and classified some 150 forms into 25 genera in 5 families. There exist, however, more than 10 additional genera described by LUTKEVICH, NOVOZHILOV, MARLIÈRE and others.

Fossil Estherians are so similar to living ones, especially to Caenoestherids, Leptestherids and Cyzicids that I fail to find any generic distinction in carapaces common to any of the living Estherian genera. Furthermore a great variability of the carapace was found in "*Estheria*" *middendorfii*. Because RÜPPEL's *Estheria* is an invalid name and because no proper substitute was found, HUZITA and I proposed *Estherites* for fossil *Estheria*.

Although taxonomic distinction is more easily made for the Leaians, the classification of Estherians is more difficult and almost impossible until some specialist like JONES undertakes extensive and intensive researches from palaeontological as well as neontological viewpoints.

Fossil Estherians are such a difficult group to work out. I have looked over all of the Estherian collections on hand, but fundamental questions remain for some one who will take them up as his life-work to solve. Bibliography and specific and generic lists are annexed to this volume, with the hope that some students will take up the problem where I have left it.

In preparing the lists I was astonished to find many aberrant forms, especially in the Leaians. Several new genera erected for them are each represented by one or a few species. Nevertheless they are well justified by their characteristics. The classification proposed here is as yet more taxonomic than phylogenetic, and I fear my comments on foreign species chiefly on the basis of their description and illustration are superficial.

My manuscript on this work was once completed in 1946, and has since been gathering dust in a drawer because it was difficult to get it published. In the last few years I began a revision of the manuscript. In the meantime I went as a Japanese delegate to the 19th International Geologic Congress at Alger, 1952. "*Estherian evolution and orogenic cycle*" read at the meeting of the International Palaeontological Union held at the same time was a summary of the result achieved up to that time. Taking advantage of the meetings, I made what was to me my second round trip of the world which

gave me the opportunity to see the literature on the subject which is not available in Tokyo. Unfortunately I cannot refer to the results of recent studies on Conchostracan fossils in Northern Eurasia, but I tried in this paper to bring together all of the salient facts insofar as they have been available to me.

Through a world-wide census of the creature I was led to the conclusion that the rise and fall of the Conchostraca are intimately related to crustal movements. I have investigated the relation of Estherian development to the orogenic cycle in Eastern Asia. As shown in the third chapter, biological cycles of the limnobios paralleled orogenic cycles, syn- and inter-orogenic faunas having their own characteristics. Then, other continents are brought into consideration in an attempt to elucidate the differences in Conchostracan history as between kratonic terrains and orogenic zones. The Earth is truly the mother of land life.

In such a research, problems must be investigated from various angles. Non-marine ecology is an important field as discussed in the second chapter. The history of the Conchostraca is influenced not only by endemism due to isolation of their habitat by crustal movement, but also by climatic changes. Climate or water temperature in the hot season is known to be the prime factor in controlling their distribution. As for their world-wide distribution, dispersal of egg capsules by wind and their durability should not be overlooked.

In short, Conchostracan classification is not the sole subject of this study. Rather it is a synthetic study on Conchostracan palaeontology. Therefore the larger part of this volume contains various subjects all of which have bearing and are necessary in understanding the history of their development. These descriptions and discussions are followed by notes on phylogeny and classification. While marine palaeoecology, especially of neritic life, is a pet subject of modern palaeontology, not much attention is paid to non-marine palaeoecology. I have tried to take up this subject in so far as the Conchostraca are concerned. Together with my papers on the late Palaeozoic and Mesozoic floras and climatology of Eastern Asia (1942, 52) and on Radiolarian rocks (with KIMURA, 1944), it is hoped that this study will contribute to the palaeoecology of geobios, limnobios and the bathyal fossil-coenosis.

As I write these words the untimely death of two of my most able students comes to my mind. I record here the deep sense of gratitude which I feel toward the late Asahi HUZITA and the late Kei-

ichi TANI who, together with Messrs. Yuho KIDO and Hisashi KUSUMI, gave me invaluable assistance and cooperation in the course of this study.

In my trip around the globe in 1952–53, I was given access to rare publications and materials in Europe and North America, and it was truly regrettable that I just did not have enough time to study the many type specimens abroad. Several photo-copies and some reprints were given me by my friends. My collection of some specimens of recent Estherians was a gift from Prof. UENO and Dr. KURODA. I wish to take this opportunity here to express my sincere gratitude to all these men, especially to

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CHAPTER I

Classification of the Fossil Conchostraca

1. What is a fossil Estherian?

Posidonia minuta VON ZIETEN, 1833, *Cyclas subquadrata* SOWERBY, 1836, and *Posidonia alberti* VOLTZ, 1837, are the three fossil Estherian species described before *Estheria* was instituted by RÜPPEL in STRAUSS-DÜRCHHEIM, 1837. As can be recognized from these generic references, Estherian carapaces present typical examples of homoeomorphism with *Posidonia* (or *Posidonomya*), *Sphaerium* (or *Cyclas*), *Halobia* (or *Daonella*), *Inoceramus* and several other pelecypods. Likewise *Leaia* and *Estheriella* are based on *Cypricardinia leidyi* LEA, 1855 and *Posidonia wengensis* GIEBEL, 1857, non WISSMANN, 1841, respectively.

There can be, however, no taxonomic confusion of the Conchostraca with the Pelecypoda, when the absence of hinge teeth is ascertained, or when the so-called Estherian ornament is seen in the interspace between growth lines, or when the chitinous (or cornious) test of the carapace can be recognized. Like a prodissoconch, the umbonal area is sometimes smooth and swelling, but its center happens to lie below the dorsal margin, an aspect never seen in pelecypods.

Little is known of the carapace structure of fossil Estherians. Some carapaces I examined suggest that the carapace consists of double layers and the so-called surface sculptures may be reliefs on the inner side. Explicit examples are found in *Estherites mitsuishii* in which growth ridges and punctae in interspaces between growth lines are found on its exfoliated surface (KOBAYASHI and HUZITA, 1942, pl. 2 and 6). In living Conchostracans it is known that the chitinous carapace is somewhat calcified.

In *Caenestheria davidi* which I examined one valve is composed of two layers, the outer one being thicker and stronger than the inner one which is a soft thin film that merges with the cuticle of the soft body in the umbonal part. Dried carapaces of *Caenestheriella gifuensis* at hand are very flexible and the two valves are fused with each other along the dorsal margin without any hinge apparatus, but so tightly that it is not easy to separate them along the dorsal margin. When I tried to separate them, a crack ran into the valve, instead of along the dorsal margin.

There is a long break in palaeontological records between the Mesozoic and older Estherians on one side and living ones on the other, but the former must be ancestral to the latter, as can be seen on soft bodies preserved in rare instances. According to BILL (1914), *Estheria minuta* (?) or *E. alberti* from the Buntsandstein of Alsace has a fornix, antenules, antennae, mandibles and a telson.

In *Limnestheria ardra* WRIGHT (1920) from the Upper Carboniferous in the Kilkenny coal-field in Ireland, antennae, claspers, mandibles and a telson are well preserved, segmentation is observable to some extent and cilia are seen along the periphery of the carapace. He has 24 specimens all similar to one another. Their appendages are of the Estherian type; although the second clasper can not be seen, one leg is a clasper in 6 specimens which are thought to be males; and if a doubtful growth band near the periphery is excluded, the surface of the carapace is smooth, notwithstanding the preservation of cilia. These aspects reveal a close alliance to *Limnetis* (i.e. *Lynceus*) and *Cyclestheria*, but the second clasper is absent. Therefore *Limnestheria* was instituted by WRIGHT for this monotypic species.

The third is *Lynceus* (*Limnetis*) *stchukini* CHERNYSHEV (1940) from the Cretaceous on the right bank of the Daya river above the Shevya village, Transbaikalia. As this generic reference suggests, there is no growth line on the surface, Two long multiarticulate appendages protrude forward from the carapace beside the filaments or the terminals of antennae. A furca (?) also multiarticulate and bifurcate behind in the form of a hook, is found detached from the carapace on the rear side. Thus it is certain that *these fossils belong to the Conchostraca*. The carapace aspect is taken into account in the neontological classification of the Conchostraca, but more weight is laid on the body, especially on the second antenna and telson, and the number of legs and segmentation of the trunk are brought into consideration. The antenna and rostrum in the head, legs, telson and other parts of the soft body are, however, generally unpreserved and the relative position of the body to the carapace is also indeterminable in fossil Estherians.

The absence of growth lines provides a practical test for distinguishing the Lynceidae from the remainder. The backward recurving of growth lines frequently seen in the Limnadiidae, especially the crenulation of the dorsal margin due to a series of short spines in *Limnadopsis* is significant. Muscular scars and shell glands are developed and well marked on the carapace in the Limnadiidae but not in

Limnadopsis.

PACKARD's Estheriidae (1874) are preceded by BAIR's Limnadiidae (1840). As the Caenestheriidae and Leptestheriidae used to be combined into SARS' Estheriidae or PACKARD's Estheriinae (1883), the two families by DADAY DE DEÉS to which most fossil Estherians are similar, have carapaces so alike that they are hardly distinguishable. The Cyclestheriidae are quite different from them in the subcircular outline of the carapace and the smaller number of growth lines, but the family is represented by the monotypic species, *Cyclestheria hislopi* SARS.

Estherian eggs (?) are reported to occur in association with *Estheria middendorfii* and *E. cebenensis*. In one of CHERYCHEV's specimens of *C. stchukini* separate minute round grains, 0.14 mm. in diameter, form a round spot 1 mm. in diameter in the posterior part where the egg of *Lynceus* are kept.

2. Neontological classification of the Conchostraca

Living Estherians are classified into 5 families and 14 genera beside some subgenera as follows:

Family Lynceidae STEBBING
- *Lynceus* MÜLLER (*Limnetis* LOVÉN, *Hedessa* LIÈVEN)
- *Lynceiopsis* DADAY DE DEÉS

Family Limnadiidae SARS
- *Limnadia* BRONGNIART
- *Eulimnadia* PACKARD
- *Limnadella* GIRARD
- *Limnadopsis* SPENCER and HALL

Family Cyclestheriidae SARS
- *Cyclestheria* SARS

Family Cyzicidae STEBBING (Caenestheriidae DADAY DE DEÉS)
- *Cyzicus* AUDOUIN
- *Eocyzicus* DADAY DE DEÉS
- *Caenestheria* DADAY DE DEÉS
- *Caenestheriella* DADAY DE DEÉS

Family Leptestheriidae DADAY DE DEÉS
- *Leptestheria* SARS
- *Leptestheriella* DADAY DE DEÉS
- *Eoleptestheria* DADAY DE DEÉS

3. Morphology of the Estherian Carapace

With reference to DADAY DE DEÉS' monograph in addition to a few other papers, I examined over 100 species in 7 genera of the Cyzicidae and Leptestheriidae, with the assistance of HUZITA (1943), to see if there is any generic characteristic in carapaces. It should be noted here that the terms, (1) caenestherids, (2) cyzicids and (3) leptestherids, will be used hereafter to comprise (1) *Caenestheria* and *Caenestheriella*, 2) *Cyzicus* and *Eocyzicus* and 3) *Leptestheria*, *Leptestheriella* and *Eoleptestheria* respectively. Furthermore, the term *form* is used for species, variety or forma.

a. *Size and outline*:—Large living Estherians are generally 12 to 16 mm. long and 7 to 8 mm. high. The largest is *Eoleptestheria ticinensis*, 20 mm. long and 13 mm. high, but even this is smaller than the largest of fossil Estherians. The height-length proportion of living Estherians ranges from 1 : 1.1 to 2.1. In caenestherids and cyzicids it is in a range 1 : 1.2 to 1.8, mostly 1 : 1.3 to 1.7, whereas it is 1 : 1.4 to 2.2 in leptestherids. In other words leptestherids have longer outlines.

Outline and convexity of a carapace are related to the soft part embraced therein. The carapace breadth attains 8 mm. in *Cyzicus jonesi*, but the true breadth of a fossil carapace is frequently difficult to determine because it is easily flattened secondarily in different degrees. Except in *Lynceus* the body is completely enclosed in two valves, but this too is difficult to ascertain in fossil Estherians.

DADAY DE DEÉS (1915) proposed three terms,—*cycladiformes*, *telliformes* and *biformes*. In the first a dorsal margin forms an obtuse angle with the posterior margin, while the two margins gradually merge one with the other in the second. As the third means sexual dimorphism between the first and the second, presence or absence of the angle cannot provide a generic distinction. More significant is the recurving of the posterior margin near the dorsal margin commonly seen in the Limnadiidae for which I propose *Limnadiformes*.

b. *Growth lines and cilia*:—Except *Lynceus* without growth lines, all Estherians retain their carapaces at the time of moulting (KUKENTHAL, 1927). Subsequent outgrowth is made along the margin of the carapace with the result that incremental bands are imbricated along

growth lines. The lines are relatively few and the umbonal area is large and smooth in the Limnadiidae.

Most of the Cyzicidae and Leptestheriidae have 7 to 30 lines, but over 50 lines are found in *Caenestheriella* and 90 lines in *Cyzicus*. It appears to be a general tendency for growth lines to be more numerous in the female than in the male. Some growth lines correspond to moultings, but many others are possibly produced in their intervals by variations in nutrition, or in outgrowth between the day and the night, or the like. It is sometimes found in fossil Estherians that certain growth lines are much stronger than others in the interspace. It is probable that most of the strong ones mark off moultings and the weak ones were made during the intervals.

Among living Estherians cilia are occasionally found along the ventral margin and also on the growth lines close to the margin, although ciliated forms seem less common than non-ciliated ones. There is no ciliate *Eoleptestheria*, but this may not be a good criterion because the genus is represented by only three species. While there is no surface-sculpture, cilia are preserved in *Limnestheria ardra*. Cilia are clearly shown by JONES (1863) in his *Euestheria middendorfii*, but are so delicate that they are rarely preserved in fossil Estherians.

In 24 forms of *Caenestheriella* there are 14 forms having a row of spots or nodes along their ventral or dorsal side. In *Cyzicus* (?) *newcombi* there are very narrow growth bands having median lines. This kind of growth line is not uncommon in fossil Estherians, but at the same time it should be noted that narrow growth bands with and without median grooves are sometimes found on the same valve.

c. *Sculpture*:—Except smooth *Leptestheria hendersoni* living Estherians have various kinds of sculptures in the interspace among growth lines, such as punctae, granulae, radial lirae, polygons, reticulae or oblique wavy lirae which can be classified into some 20 types as illustrated in figure 1.

The sculpture is not always the same through growth. *Caenestheria bouvieri* has the *sibirica* type of sculpture in its young stage but when spots become larger, it turns into the *californica* type. In *Caenestheria rubra* the *sibirica* type of sculpture develops into the *madacascarica* type by acquiring large spots. *Leptestheria aegyptica* on the other hand shows a change from a type of *aegyptica* to its "b" type through growth, the change being the appearance of fine punctae within the

reticulae. A change from the *siliqua* type to the *cortieri* type is seen in the growth stages of *Leptestheria mayti*.

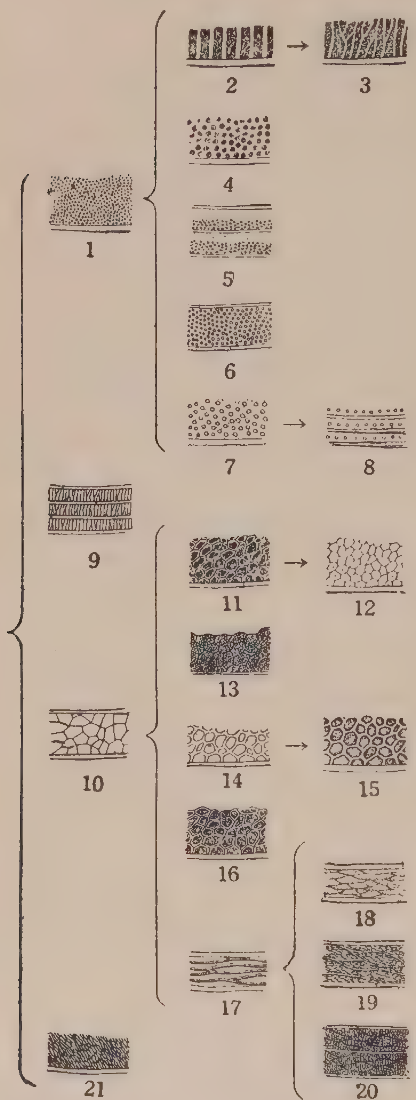


Figure 1. Various types of sculptures in living Estherians.

(See Table 1 for the names of these types.)

Furthermore the sculpture tends to change from the *packardi* type to the *ehrenbergi* type in *Caenestheria cinita* and *Caenestheriella elizabethae*. In *Caenestheriella ehrenbergi dimorpha* the dendritic grooves become complicated in the full grown stage. A particularly interesting form is *Caenestheriella paradoxa* in which the sculpture changes from the *sibirica* type to the *ehrenbergi* type and later from the latter to the former. The sculpture is different between the male and the female in a few forms. In *Leptestheriella thielei* for example the female has the *siliqua* type and the male has the *packardi* type of sculpture.

Although it is not yet quite certain, the development of the sculpture may be deduced from the morphological series as follows:

1) appearance of spots or striae.
2) enlargement of spots.
3) appearance and disappearance of grooves.
4) change of grooves from radial to dendritic.
5) change of pattern from polygonal to reticulate.

The sculpture bears an intimate relationship with the cellular arrangement of the hypodermis, because each polygon corresponds to each hypodermal cell whence chitinous material is secreted (KÜKENTHAL 1927).

Table 1. The number of forms of living Estherians having different types of sculptures.

(x) means the number of forms of doubtful reference.
[x] means the number of immature forms.

	Group		Caenestherids		Cyzicids		Leptestherids		
Group of sculpture	Genus / Type of sculpture		*Caenestheria*	*Caenestheriella*	*Cyzicus*	*Eocyzicus*	*Leptestheria*	*Leptestheriella*	*Eoleptestheria*
	0	*hendersoni*	1						
sibirica	1	*sibirica*	7	4(+1)	15(+7)	1(+2)	1(+1)	1(+1)	
	2	*packardi*		4					
	3	*ehrenbergi*		8	1				
	4	*orientalis*				6	1		
	5	*lofti*			1				
	6	*californica*	1	1	2				
	7	*madacascarica*	2	2					
	8	*jonesi*			1				
	9	*similis*		1					
braueri	10	*braueri*	1				5		1
	11	*venezelica*					2		
	12	*immsi*	1						
	13	*dahalacensis*					3		
	14	*calcarata*					1		
	15	*chinensis*						1	1
	16	*divis*						1	
	17	*aegyptica A*					[1]		
	18	*aegyptica B*					1		
	19	*cortieri*					2		
	20	*compleximata*					1		
	21	*vanhöffeni*					1		

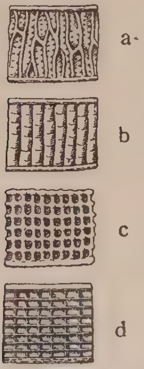
Table 1 inserted here shows the number of forms having these sculptures. Putting aside the *hendersoni*, *similis* and *vanhöffeni* types of sculpture which are each represented by one form, the following facts cannot be overlooked.

1) Most leptestherids have reticulae i.e. the *braueri* group of sculptures. They are found also in a few caenestherids, but not in cyzicids.
2) Most caenestherids and cyzicids have punctae or granulae i.e. the *sibirica* group of sculpture.
3) Many forms of *Cyzicus* have sculptures of the *sibirica* type, but the same sculpture is not uncommon among caenestherids.
4) The *orientalis* type of sculpture is practically restricted to *Eocyzicus*, and more than two-thirds of the genus have it.
5) Grooves of the *packardi-ehrenbergi* type are found most frequently in *Caenestheriella*.

In summarizing the above facts, it may be said that.

1) Caenestherids and cyzicids commonly have spotted sculptures, whereas leptestherids frequently possess reticulated ones.
2) Carapace is generally more elongated in leptestherids than in the two other groups.

If a carapace belongs to the cyladiformes not elongated, its umbo located within the anterior third of the dorsal margin and growth lines have a row of spots, the *packardi-ehrenbergi* type of sculpture being found in the interspace, then it is quite probable that the carapace belongs to *Caenestheriella*, but not all of *Caenestheriella* show these characteristics.



a. *Euestheria kotahensis* (JONES), 1862, pl. 2, fig. 25.

b. "*Estheria*" *ovata* by JONES, 1862, pl. 2, fig. 36.

c. *Euestheria colombianus* (BOCK), 1953, pl. 13, fig. 7.

d. *Euestheria tessellata*, (JONES), 1891, pl. 5, fig. 46.

Figure 2. Some types of fossil Estherian sculptures.

A certain aspect of the carapace is commonly met with in a genus or a group of genera. Such aspects are, however, not always seen in the genus or group. At the same time the aspect can also be found in the other genus or group of genera. Therefore no character-

istic of the carapace is absolutely decisive for generic identification, and *there is no criterion identifying a fossil carapace definitely with any of the recent genera.*

Beside these types of sculptures there are several others in fossil Estherians. For example, reticulae in parallel rows, but alternating side by side in *Euestheria minuta brodieana;* regular rectangular mesh, as seen in *Euestheria tessellata, Euestheria bianneyana, beinertiana* and *E. berryi*. *Euestheria totahensis* has radial lirae as well as fine punctae in their intervals. The size of polygons becomes smaller near the periphery in *Euestheria adamsi* and radial lirae and reticulae both occur in the same interspace in *Euestheria middendorfii.*

DEPÉRET and MAZERAN (1912) suggested that fine punctation develops into reticulation. What type of sculpture is really the most primitive and what is the genetical relationship among various types of sculpture, are important questions for those who study the carapace, although they may not be of much interest to neontologists.

4. Sexual dimorphism and endemic polymorphism.

While parthenogenesis is the characteristic mode of reproduction in the Notostraca and common in the Cladocera, reproduction is generally made sexually in the Conchostraca, like in the Anotostraca. Therefore there are males and females which are in many species more or less different in the size and outline of its carapace.

Let me take up here the discussion of sexual demorphism of fossil Estherians from Asiatic species with which I am familiar. Most of *Estherites mitsuishii* (KOBAYASHI and HUZITA, 1942) have some 20 growth lines, but some have more than 30. The height-length proportion ranges from 1; 1.1 to 1.6; dorsal and ventral margins usually subparallel to each other; umbo is fairly large, projected a little above the dorsal margin and located at a subcentral position relative to the margin as well as the valve. Its sculpture is a kind of irregular mesh-pattern, or dots of negative impression.

Two forms of this species are always found together. The outline is more variable in the common form but uniform in the uncommon form. Growth lines are less in number in the former than in the latter. Otherwise the two forms are identical and their maximum sizes are about the same.

As noted elsewhere (KOBAYASHI and KUSUMI, 1953), the female is

shorter than the male in *Eocyzicus mongolianus* UENO. Its dorsal margin is straight in the male whereas it is slightly convex upward and the carapace is relatively broad in the female. This is because, aided by dorsal projections of posterior legs, eggs which are agglutinated by a sticky substance, are kept in the postero-dorsal part between two valves for a few days or a week before being freed from the carapace.

Such an arcuate dorsal margin is found also in the females of *Caenestheria davidi* (SIMON), *Eoleptestheria chinensis* DADAY DE DEÉS and many other living Estherians. The female is narrower in *Leptestheria kawachiensis* UENO, but the reverse is the case in *Caenestheria gifuensis* (ISHIKAWA). FISHER and JONES noted that the male is broader than the famale in *Estheria hierosolymitana* and some other species. CHI recognized a similar difference in the Chinese material.

The height-length proportion is almost constant in the uncommon form of *E. mitsuishii*, suggesting that it is male. But the carapace dimensions range from 6 mm. to 9 mm. in length and from 4.5 mm. to 6 mm. in height in the uncommon form and from 4.5 mm. to 8.5 mm. in length and 4.5 mm. to 6.5 mm. in height in the common form. This fact suggests that the common form is male.

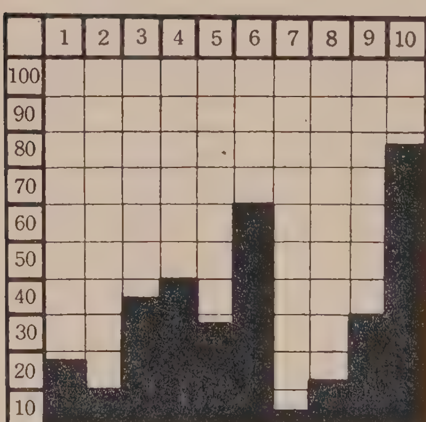


Figure 3. Individual ratio between males and females of *Leptestheria dahalacensis* (after SPANDL)

1. Praterau bei Wien
2. Au bei Kolosterneurberg
3. Tümpel bei Spillerum
4. Tümpel bei Tullen
5. Tümpel bei Korneuberg
6. Tênênir, Asia Minor
7. Tümpel bei Münchendorf
8. Tümpel bei Parndorf (Burgenland)
9. Tümpel bei Apetlon (Burgenland)
10. Aleppo, Asia Minor.

All localities in Lower Austria except 6 and 10. Every 100 specimens at one locality are examined and the percentage of the individual number of males to the total is shown in column.

UENO however informed me of his experience in collecting living Estherians, saying that males are rare but females are abundant, males and females being found roughly in the ratio of 1 : 3. If this can be applied to *E. mitsuishii*, the common form must be female.

The ratio between males and females varies greatly, however,

according to ecological condition. Through a survey of *Leptestheria dahalacensis* at 8 localities in Lower Austria and 2 in Asia Minor SPANDL (1925) found that the percentage of males in the total number varies from 10 percent to over 85 percent. According to him it is a general tendency for the percentage to increase in the warm region. (See figure 3.) Unless the ovarium is preserved, therefore, it is very difficult to decide which is male and which female. Nevertheless it is highly probable that *the two forms of E. mitsuishii reveal sexual dimorphism of an identical species.*

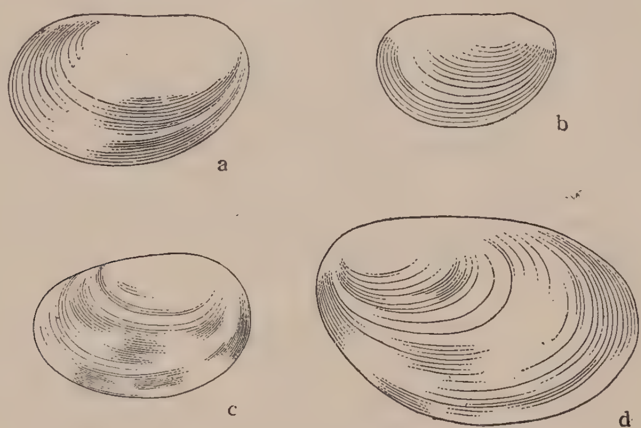


Figure 4. Polymorphism of *Euestheria kyöngsangensis*

a. *Euestheria kyöngsangensis* var. *medialis* KOBAYASHI and KIDO
b. *Euestheria kyöngsangensis* var. *paucilineata* KOBAYASHI and KIDO
Both from the Kansenri formation
c. *Euestheria kyöngsangensis* var. *huzitai* KOBAYASHI and KIDO
d. *Euestheria kyöngsangensis* (KOBAYASHI and KIDO)
Both from the Shikkoku formation

Another example of possible sexual dimorphism is found in *Euestherias kyöngsangensis* (KOBAYASHI and KIDO 1947). From a morphological standpoint the species can be classified into 4 forms, namely var. *huzitai*, var. *medialis* and var. *paucilineata* beside the typical form. The typical form and var. *huzitai* are found together in the Shikkoku formation of the Lower Cretaceous Naktong series at Kotanri in South Korea. They have the same kind of sculpture and about the same number of growth lines, but differ in outline. Var. *huzitai* is taller and ovate in outline, dilating forward. Because it resembles *typica* closely, it was taken for a variety, but they are possibly sexually dimorphic.

Two other varieties, *medialis* and *paucilineata*, are found together at Akari in South Korea in the Kansenri formation of Middle Cretaceous Shiragi series. While growth lines are estimated to be 35 or more in the Shikkoku forms, the number fluctuates from 25 to 30 in var. *medialis* and from 15 to 20 in var. *paucilineata*. Furthermore the last one is different from the three others in its subelliptical outline. As noted already, *medialis* and *paucilineata* may be a case of sexual dimorphism. Therefore the morphic change from the Shikkoku pair to the Kansenri pair possibly indicates the mutation of WAAGEN, 1868, non DE VRIES, 1901.

The morphic variation of *Euestheria middendorfii* (JONES) is more complicated. Jointly with KUSUMI I studied the collection of the species procured from the Jehol group at 15 localities in Manchuria and Korea. As described in detail in a recent paper (1953), it comprises 3 varieties and 4 formae beside the typical form and there is no sharp boundary among them. Two forms in different combinations are found at 4 localities, 3 forms at another locality and 4 forms at still another.

The collection of Fengshen in Jehol is the last case where forma *intermedia* is abundant, var. *chii* and forma *orientalis* are common and var. *elongata* is rare. They can be two dimorphic pairs. It is also possible that var. *elongata* inclusive of the two formae is a case of sexual dimorphism relative to var. *chii*, because var. *elongata*, forma *orientalis* and forma *intermedia* are very similar to one another, but fairly distinct from var. *chii*. In the Takechen collection the typical form is abundant and var. *jeholensis* and var. *chii* are rare. Because var. *jeholensis* forms a continuous series with the typical form, it is not improbable that the typical form plus var. *jeholensis* is dimorphic with var. *chii*.

These are, however, no more than a possibility. Much still remains to be studied on the polymorphism of *E. middendorfii*, because they are widely distributed in Asia from Sinkiang in the west to Korea in the east and from Transbaikalia in the north to Central China in the south in various formations from Middle Jurassic to Upper Jurassic or probably to Lower Cretaceous.

Insofar as the morphic divergence of *E. middendorfii* is concerned, various forms appear to form a large *Rassenkreis* as proposed by RENSCH (1934) for the Cladocera which, however, comprises not only *geographische Rassen* but also geological races, because morphic dif-

ferences presumably depend in part upon endemism as well as mutation. In my opinion the variations, geographical and geological, are mixed together in this case with sexual dimorphism to produce a picture of polymorphism.

Still more puzzling is the Estherians from the Cretaceous Inkstone formation. According to HASE's preliminary study (1948) of IMAMURA and KUSUMI's collection from the Yamaji shale at Inakura in Prov. Bitchu (IMAMURA and KUSUMI, 1951), there are different forms which are connected by intermediate forms. His d, d_1 and g forms are respectively similar to *E. kyöngsangensis*, *E. kyöngsangensis medialis* and *E. naktongensis*. His a, b and c forms whose length divided by height is about 1.15, 1.15 and 1.10 to 1.15 respectively, are tall, but f form (L/H, 1.9–20) is broad.

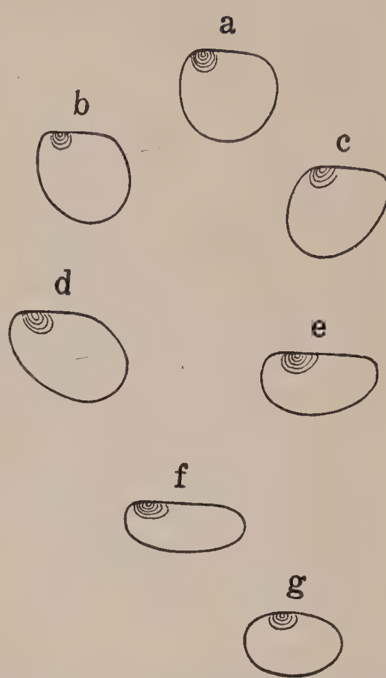


Figure 5. Polymorphism of some Estherians from the Cretaceous Inkstone series at Inakura, Prov. Bitchu.

Eliminating the g form or *E.* cfr. *naktongensis* which is fairly distinctly isolated from the remainder, the umbonal position varies one-third to one-sixth of the length from the anterior end of the valve among the remaining forms. Because they are found together at the same locality the difference can be attributed to neither endemism nor mutation. If the range of variability is really so great within a species, it can hardly be defined.

It is known, however, that the height-length proportion of recent species at each locality is well defined, as examplified in *Eulimnadia braueriana*, *Leptestheria kawachiensis* and *Caenestheria gifuensis* (KOBAYASHI and KUSUMI, 1953), although the last species shows variations in carapace-size according to habitat (KOBAYASHI and KUSUMI, 1953).

Because this is so unusual, I once visited Inakura and found that the fossils in question are deformed secondarily not to a small extent. Therefore it is probable in this case that there are at least three species and polymorphism is here complicated by dimorphism and deformation.

Finally I wish to present a few examples. Two forms of Estherians occur in the Tendaguru formation in Tanganika district in Africa. One is an elongate form (L/H, 1.8) and the other well rounded (L/H, 1.07). If such a wide difference is attributed to secondary deformation (JANENSCH, 1933), no exact concept of the species is obtainable. I think it proper to give a new name for the round form in fig. 2, restricting *Euestheria tendagurensis* (JANENSCH) to the elongate form (fig. 1). With grateful memories of his kind assistance during my vist to Berlin in 1934 to study the Eo-Palaeozoic fossils in RICHTHOFEN's collection, I denominate the round form as *Cyclestherioides janenschi*, new species, in honour of Prof. W. JANENSCH of the University at Berlin. In this species the carapace is well rounded in outline except the dorsal margin which is straight and on which the umbo is located terminally and somewhat acuminate. The valve is longest at mid-height and highest at mid-length.

They were collected from the upper Dinosaurian beds, younger Mesozoic or Purbeckian in age. It is interesting to note that *E. tendagurensis* and *C. janenschi* are respectively similar to *Euestheria kawasakii* and *Cyclestherioides koreanica* in the Carnic of Japan and Korea. Although the two African species are found in association, I can not consider them to be sexually dimorphic, because they are so different as to make generic distinction possible. For the same reason I fear that *Estheriella circularis* and *E. elliptoidea* can not be combined in *Esteriellites elliptoideus* as sexual dimorphism (BOCK, 1953).

In short *sexual dimorphism cannot be said to be extensive in living Estherians and which is male and which female is not easy to say in fossil Estherians.* It is sometimes difficult to grasp the specific concept of fossil Estherians because of a high degree of polymorphism due to endemism, mutation and sexual dimorphism, in addition to secondary deformation.

5. Estheria RÜPPEL, 1839, an invalid name

It is certainly unfortunate that *Estheria* which has been widely used for a Conchostracan genus, cannot be used because it is preoccupied by *Estheria* ROBINEAU-DESVOIDY, 1830, an insect genus. *Estheria dahalacensis* RÜPPEL which is the type of his genus is now referred to *Leptestheria* SARS, 1898.

Isaura JOLY, 1841, is thought to be also invalid, because it is a

synonym of *Isaura* SAVINGNY, 1817. The type of JOLY's genus is *Isaura cycladoides* JOLY which is now referred to *Cyzicus* AUDOUIN, 1837. AUDOUIN did not give any generic diagnosis, but *Limnetis tetraceras* KRYNICKI must be the type species of *Cyzicus* (RAYMOND, 1946). Thus *Cyzicus* and *Isaura* are synonymous, the former having been denominated prior to the latter. I do not intend to go any further in the nomenclature of living Estherians, but it is certain that *Estheria* is invalid. BOCK intends to substitute *Isaura*, emphasizing that *Cyzicus* has never been described. If *Cyzicus* were invalid, *Isaura* must be substituted for *Cyzicus*, instead of fossil *Estheria*.

As I have already shown, there is no definite characteristic in the the carapace by which any genus of the Cyzicidae or Leptestheriidae can be distinguished. Therefore the application of *Leptestheria*, *Bairdestheria* or any other recent generic name to fossil Estherians is not tenable. For this reason I proposed *Estherites* in 1943 jointly with HUZITA on the basis of *Estheria mitsuishii* KOBAYASHI and HUZITA. At that time I had no idea of *Asmussia* PACHT, 1849, DEPÉRET and MAZERAN's *Euestheria* and *Lioestheria*, 1912, and *Palaeestheria* BERNARD, 1929. Now I think that *Estherites* is a valid genus of the Lioestheriidae RAYMOND, as discussed later.

Lately EDWARDS and STUBBLEFIELD (1948) suggested *Euestheria* as the collective name for fossil Estherians. Prior to them RAYMOND (1946) split fossil Estherians into many genera, as mentioned below.

6. Fossil Conchostracan genera and families

Fossil *Estheria*, *Estheriella* and *Leaia* have long been placed in the Limnadiidae by JONES, ULRICH, BASSLER and others, but fossil Estherians are more allied to the Cyzicidae and Leptestheriidae. In ZITTEL-BROILI's *Grundzüge* (1924) these three genera are placed in the Estheriidae which are invalid because *Estheria* is invalid. RAYMOND's revision on the fossil Conchostraca (1946) is the most comprehensive one since JONES' monograph. He classified Estherians into 20 genera in 4 families and Leaians into 4 genera in a new family aside from *Rhabdostichus* of unknown position for which RUSCONI (1946) later proposed the Rhabdostichidae. RAYMOND's scheme of classification is as follows :—

1. Family Cyzicidae STEBBING
   Bairdestheria RAYMOND

2. Family Lioestheriiaae RAYMOND
   Lioestheria DEPÉRET and MAZERAN
   Erisopsis RAYMOND
   Asmussia PACHT
   Orthothemos RAYMOND
   Euestheria DEPÉRET and MAZERAN
   Pseudestheria BERNARD
   Estheriella WEISS
   Dadaydedeesia RAYMOND
   Monoleiolophus RAYMOND
3. Family Lynceidae STEBBING
   Lynceus MÜLLER
4. Family Limnadiidae SARS
   Palaeolimnadia RAYMOND
   Pemphicyclus RAYMOND
   Estheriina JONES
   Limnestheria WRIGHT
   Limnadopsis SPENCER and HALL
   Palaeolimnadiopsis RAYMOND
   Anomalonema RAYMOND
5. Family Cyclestheriidae SARS
   Cyclestherioides RAYMOND

x. Family unknown
   Rhabdostichus RAYMOND

6. Family Leaiadidae RAYMOND
   Leaia JONES
   Hemicycloleaia RAYMOND
   Paeleaia LUTKEVICH
   Paraleaia RAYMOND

Among them *Erisopsis* RAYMOND, 1946, is preoccupied by *Erisopsis* MOEHRING, 1858, in the Aves (SCHULZE and KUKENTHAL, 1920). There are in addition the following 12 genera, subgenera inclusive, and 3 families which he overlooked or which were described after his revision.

Acantholeaia ALMEIDA
Cornia LUTKEVICH
Diaplex NOVOZHILOV
Diaphora NOVOZHILOV
Echinestheria MARLIÈRE

Esheriellites BOCK
Estheriopsis RUSCONI
Estherites KOBAYASHI and HUZITA
Howellites BOCK
Metaleaia KOBAYASHI
Polygrapta NOVOZHILOV
Vertexia LÜTKEVICH
Estheriellidae KOBAYASHI
Isauridae BOCK
Rhabdostichidae RUSCONI

Incidentally, *Diaphora* NOVOZHILOV, 1946, is a homonym of *Diaphora* STEPHENS, 1828 (Lep.), *Diaphora* MACQUART, 1834 (Dipt.), (SHERBORN, 1801–1850, p. 1900), and *Diaphora* LÖW, 1878, (Rhynch. Psyll.) (SCHULZE and KUKENTHAL, 1920).

7. Taxonomy of fossil Estherians

I agree with RAYMOND (1946) that "at the present time it would be unsafe to place any of the Palaeozoic fossils in modern genera". This statement is equally true for the Mesozoic Estherians because there is no linking form in the Tertiary. As RAYMOND complained, fossil Estherians have few striking features. Namely "the outline of the valves, the curvature of the hinge, the position of the umbo, the presence or absence of a muscular scar, the spacing of the growth lines, or concentric ridges, the presence or abscence of radial marking and the minute markings on the shell, reticulations, spinules, or puncta, are the only characteristics which the palaeontologist can study". With this kind of material it is certainly difficult to distinguish 35 genera.

The Lynceidae have no growth lines on the carapace, and the reference of such a carapace to the family is the best one can do. But the generic reference of Cretaceous *Lynceus* (*Limnetis*) *stchukini* cannot be warranted, even though a few appendages are preserved.

Growth lines are few in the Limnadiidae and Cyclestheriidae. Most of the former have a large smooth umbonal area and a few incremental bands near the periphery. In the genera which RAYMOND has referred to the Limnadiidae, however, the smooth umbonal area is much smaller or absent. When absent, the growth lines are fairly numerous. Furthermore it happens frequently in fossil Estherians that growth lines on the umbonal side are effaced secondarily. There-

fore the presence or absence of these lines is not quite a practical distinguishing feature.

The outline of the carapace is circular in *Cyclestheria*; hence the names, *Cyclestheria* and the Cyclestheriidae. RAYMOND's *Cyclestherioides* is certainly similar to the genus in outline and in the number of growth lines, but there are some forms similar in outline but having more numerous concentric lines. The number is 6 or 7 in *Cyclestherioides lenticularis*, 12 or more in *Cyclestherioides cycloides*, 20 to 25 in *Cyclestherioides* (?) *proamurensis* and 24 to 40 in *Cyclestherioides rampoensis*. There are gradations from these circular forms to the broadly ovate or subelliptical forms through high ovate forms such as *Euestheria kusumii*, *Euestheria nenkiangensis kutsankouensis* and several others. Therefore the generic distinction cannot be but artificial and arbitrary.

Permian *Cyclestherioides lenticularis* is the type species of the genus which appears certainly similar to *Cyclestheria*. Looking over these Mesozoic forms of Eastern Asia and some others, however, I prefer to emend the generic diagnosis so as to include a continuous morphic series, and to erect the Cyclestherioidinae in the comprehensive Lioestheriidae, because its morphic boundary from the others of the Lioestheriidae is not so sharp as that which separates the Cyclestheriidae from the other recent families.

Among some 20 Estherian genera there are of course some form-genera which are clear-cut in one or other significant aspect. Therefore I want to commence the discussion from such aberrant genera. The most distinct genus is LUTKEVICH's *Vertexia* which has a prominent hollow spine at the umbo and another long one at the posterior end of the dorsal margin, in addition to a series of small processes at the junctions of the margin with growth lines. Test is punctate. This spiniferous genus is represented by a unique species, *Vertexia tauricornis*, from the Tatarian of Russia.

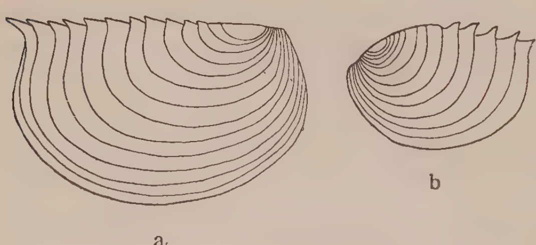


Figure 6. Spiniferous carapace of *Limnadopsis*
a. *Limnadopsis tatei* SPENCER and HALL
b. *Limnadopsis brichii* (BAIRD)

A row of similar spines is found in SPENCER and HALL's *Limna-*

dopsis comprising *L. squirei*, *L. tatei* and *L. brunneus* which were collected in Australia by the Horn expedition. The dorsal margin is straight in *L. tatei* but strongly arcuate in *L. squirei*. Because the carapace in these limnadiforms protrudes into a short spine at the posterior end of the dorsal margin, the spines of the incremental bands are aligned on the margin.

As noted by RAYMOND, his *Palaeolimnadiopsis sibericensis* (i.e. *Estheria amurensis* in fig. 5, CHERNYSHEV, 1930) may be a limnadiform apparently having spines. Its sculpture consists of radial lirae. In *Palaeolimnadiopsis kantoensis* the dorsal margin reveals a weak concavity behind the umbo and more or less protruded dorsally at the end. Its carapace possesses radial lirae in the interspace but not dorsal spines.

Although *Anomalonema reumauxi* has no spine, growth lines reveal a backward recurving. *Anomalonema* is here adapted for a Carboniferous genus of the Estheriellidae, because the radial markings are finer in it than in Lower Triassic *Estheriella* and they are not strengthened mesially as in the latter.

Echinestheria MARLIÈRE in which the small umbonal area is pointed into a short spinous process below the dorsal margin is allied to *Vertexia*. What bearing the process has on the animal is unknown. *E. marimbensis* from the Upper Triassic of Angola is its monotypic species which is a telliform without serration along the dorsal margin.

Cornia has a smooth umbonal area below the dorsal margin. Its type species must be *C. papillaria* LUTKEVICH, 1937, instead of *C. melliculum* LUTKEVICH, 1941. Because *Estheria ortoni* CLARKE, 1900, is referable to the genus, RAYMOND's *Pemphycyclus*, 1946, is a synonym for *Cornia* LUTKEVICH, 1938.

The swollen umbonal area, like the prodissoconch in the Pelecypoda, is surrounded by a flattened peripheral zone in *Estheriina* JONES, but the area is marked by fine growth lines. These protuberances of different size in *Estheriina* and *Cornia* allude to the fat juvenalium in the genera.

Thus we obtained now *Vertexia*, *Palaeolimnadiopsis*, *Echinestheria*, *Cornia* and *Estheriina* which are similar to the Limnadiidae in one or other aspect. Therefore they are tentatively placed in the family. It is, however, a question whether *Palaeolimnadiopsis carpenteri*, the type of *Palaeolimnadiopsis*, is really an Estherian, as discussed later (see page 95).

With only the carapace available the most difficult distinction to make is between the Cyzicidae and the Leptestheriidae. Although the elongated carapace with a terminal or subterminal umbo is common in the latter family, it is not diagnostic.

(1) 97 percent of the Cyzicidae has the *sibirica-similis* type of sculpture.

(2) 94 percent of the *sibirica-similis* type is found in the Cyzicidae.

(3) 83 percent of the Leptestheriidae has the *braueri-vanhöfeni* type of sculpture.

(4) 90 percent of the *braueri-vanhöfeni* type is found in the Leptestheriidae.

Therefore the carapace with punctae, granulae or radial lirae in the interspace has more than 90 percent probability of belonging to the Cyzicidae. The probability for the carapace with polygons or wavy mesh-pattern in the interspace of belonging to the Leptestheriidae is 80 percent or more. Therefore the mode of sculpture in the interspace may be an important criterion. But it is well known in *Euestheria middendorfii* that radial lirae and polygons occur in the same interspace. In other words the distinction between the *similis* and *braueri* groups of sculpture bears not even a specific value in this case.

Because I failed to find in the carapace any distinctive characteristics between the two families, I wish to adopt "Lioestheriidae" for the large group of fossil Estherians which are similar to the Cyzicidae and Leptestheriidae in addition to the Cyclestheriidae.

As discussed already, the classification of fossil Estherians cannot be anything but artificial at present. But now I am of the opinion that the creation of form-genera must be an approach to natural classification. From the same view-point RAYMOND has created 9 new genera and a new family, saying that "I have been conservative in creating new genera". From my observation on the Asiatic material he seems to me to be rather liberal, insofar as the Estherians are concerned.

The specific number of the afore-mentioned aberrant genera is very small, if compared with the remainder in the Lioestheriidae. According to RAYMOND *Bairdestheria*, *Euestheria* or *Pseudestheria* is an Estherian genus with radial lirae, reticulae or punctae respectively. Otherwise they are similar to one another in the subovate or subelliptical outline of the carapace, terminal or subterminal umbo and numerous lines of growth.

As discussed already, radial lirae and punctae are predominant

sculptures in the Cyzicidae whereas reticulae are prevalent in the Leptestheriidae. Among fossil Estherians on the other hand radial lirae and reticulae are sometimes found in the same carapace or even in the same interspace. Therefore I cannot accept RAYMOND's reference of fossil *Bairdestheria* and *Euestheria* respectively to the Cyzicidae and Lioestheriidae. Moreover it is questionable whether fossil *Bairdestheria* belongs to an identical genus with living *Bairdestheria*.

In the case of fossil Estherians punctate sculpture is fairly distinct from the two others. The distinction of *Pseudestheria* from *Palaeestheria* is based on the presence or absence of a smooth umbonal area which, however, depends frequently upon the mode of preservation, and hence the distinction is not practical. Among the punctate genera *Lioestheria* was denominated prior to *Palaeestheria* or *Pseudestheria*.

As to NOVOZHILOV's *Polygrapta*, *Diaplex* or *Diaphora* it is difficult for me to get any exact concept from his illustration or English résumé. *Polygrapta*, *Howellites* and *Estheriellites* are, however, apparently not much different from *Euestheria* and NOVOZHILOV's two other genera from *Lioestheria* in the sculpture of the interspace, although intensive studies may bring out minor differences in the future.

What kind of sculpture is predominant? The answer to this question gives us a distinguishing clue among them. *Euestheria* together with fossil *Bairdestheria*, *Polygrapta*, *Howellites* and *Estheriellites* forms a group with reticulae or radial lirae. *Lioestheria*, *Palaeestheria*, *Pseudestheria*, *Diaplex* and *Diaphora* form a punctate group. In each group the first genus has priority. *Euestheria* is, however, a sort of dumping ground for which RAYMOND used *Pseudestheria*, because any form, if its sculpture is obscure, is provisionally placed in *Euestheria*.

Because the two valves are connected with the body at the umbo and the change of its position greatly modifies the carapace and probably the body too, the umbonal position must be a more important criterion than the sculpture. Therefore the Asmussiinae with subcentral umbones are distinguished from the Lioestheriinae with terminal or subterminal ones, *Asmussia*, *Estherites*, *Orthothemos*, *Erisopsis* and *Palaeolimnadia* have central or subcentral umbones. *Asmussia* can be distinguished from *Estherites* by its tall carapace and straight dorsal margin. *Erisopsis* was proposed for the subtrian-

gular carapace the axis of which is quite oblique to the hinge. The holotype of *E. tessellata* (RAYMOND, 1946, pl. 1, fig. 7) is, however, not much different from *Asmussia membranacea* either in the outline or the obliquity of the axis and RAYMOND's *Erisopsis* is an invalid name, as pointed out already. (See page 24). *Orthothemos* can be said to be punctate *Estherites; Palaeolimnadia wianamattensis* may be *Estherites* with a smaller number of growth lines. Therefore *Asmussia* and *Estherites* are accepted here as valid genera of the subfamily beside *Quadriasmussia* on which more information will be given later. (See pages 91 and 133)

Finally *Pseudoleaia* which I based on Neocomian *Estheria rectangula* has a subquadrate outline and two diagonal obtuse ridges which are incomparably weaker than the carinae of the Leaian. In considering its isolated occurrence in such a high horizon, I would refer the genus to the Lioestheriinae rather than to the Leaiadidae.

As schematized in the 6th chapter, the Lioestheriidae are classified into the Lioestheriinae, the Asmussiinae and the Cyclestherioidinae with reference to the carapace outline and the position of the umbo. The sculpture in the interspace is adopted only for the generic distinction in the first subfamily.

8. Taxonomy of Estheriellians and Leaians

Palaeontologist sees the long history of the development of life, while Neontologist sees only its present scene. Therefore it is easy to understand how there have been many more varieties of genera and families in the past than now exist. It can easily be recongnized from radially ribbed or carinate Conchostracans. As the type species of *Leaia* and *Estheriella* were first referred respectively to *Cypricardinia* and *Posidonomya*, they are not unlike certain pelecypods, but their carapaces are chitineous or corneous.

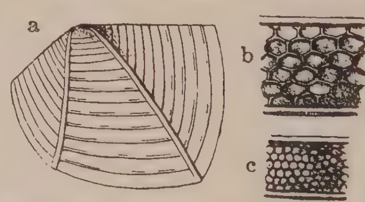


Figure 7. *Leaia subquadrata* RAYMOND (×5) and its sculptures (×40, c near the margin)

JONES (1870) called our attention to the Conchostracan sculpture of the test preserved in *Leaia leidyi* (i.e. *L. subquadrata* RAYMOND). Polygons in it become smaller near the periphery as in *Euestheria adamsi*. A similar sculpture of "*Leaia*" *unicostata* was clearly illustrated by REED (1929). Coarse punctae

exist in "*Leaia*" *monocarinata* (LUTKEVICH, 1941). As mentioned by JONES, one cannot use these sculptures as the basis for specific or generic distinction in the case of the Leaians, because it is seldom preserved. The surface of the carapace is pitted or granulated in "*Estheriella*" *nyasana*, according to NEWTON, (1910). Therefore *Estheriella* and *Leaia* must be companion genera of "*Estheria*".

The appearance of radial ornaments is quite sporadical. How they have developed and what bearing they have on the animal are two fundamental questions. At any rate, the radial ornaments are certainly remarkable characteristics because none of the living Conchostraca or living Crustacea has such ornaments on the carapace. As revised elsewhere (KOBAYASHI, 1933, 36), radial ribs are well developed in some genera of the Eopteridae MILLER. The group of *Ribeiria* has been referred very provisionally to the Phyllopoda or the Notostraca by some authors including myself. The reference of the *Ribeiria* group to the Discinocarina (RAYMOND, 1935) is not convincing because the calcareous carapace is always folded down in the group. Now I think that the group constitutes a distinct order, *Ribeirida*, nov.

Because the radials are so strange to the living Conchostraca, I agree with RAYMOND in distinguishing the Leaiadidae with a few but definite number of radial carinae or ribs from the remainder. I think it appropriate further to discriminate between the Estheriellidae with greater and indefinite number of radial ribs and Leaians or Estherians. They are two families of the Conchostraca with radial ornaments. In *Estheriella*, s. str. radial riblets are stronger on the mesio-ventral part of the valve, but die out toward the umbo and become weaker on the anteal and posteal sides. In *Leaia*, s. l. on the contrary, the radial carinae are 4 or less in number, stronger and divergent from the umbo, although the carinae sometimes die out near the ventral margin in rare instances, *Leaia latissima* for example.

Nothing is known of the soft part of *Leaia* or *Estheriella*. Nevertheless *Estheriella* is, taken as it has been for a subgenus of *Estheria*, quite similar to fossil Estherians, if the radial ornament is ignored. As RAYMOND referred *Estheriella* and *Monoleiolophus* to the Lioestheriidae, the taxonomic boundary among Estherians, Estheriellians and Leaians is by no means very sharp.

In the Estherians the sculptures in the interspaces are very fine and interrupted by growth lines. *Estheriella* has radial riblets on

the surface crossing the growth lines. The radial lirae of *Estheriellites ellipsoideus* are fairly distinct but much finer than the Estheriellian riblets, as can be seen from BOCK (1953) placing the species in his Isauridae i.e. the Lioestheriidae.

Pseudoleaia rectangula from the Neocomian of the Yuasa basin in Prov. Kii (Wakayama Pref.), Japan, is a solitary species in Eastern Asia having radial marking. Its outline is certainly similar to *Leaia leidyi*, but the two radials which YOKOYAMA (1894) called carinae consist of a gentle anterior fold and an obtuse posterior crest. Because neither a Leaian nor an Estheriellian is known from Eastern Asia or from the Jurasso-Cretaceous formation in the other parts of the world, *Pseudoleaia* must be an aberrant off-shoot of the Lioestheriidae and independent from the Leaiadidae. Since the Estheriellidae as well as the Leaiadidae are unrepresented in Eastern Asia, my own observation is quite restricted. Some comments as are here made are based principally on my study of the literature on the subject.

Accepting PRUVOST's grouping (1919), RAYMOND (1946) has split *Estheriella*, s.l. into *Estheriella*, *Anomalonema* and *Dadaydedeesia*. I have already expressed my opinion on the second. The third genus must be eliminated from the Conchostracan list, because its type species, *Estheriella radiata* (SALINA) var. *multilineata* JONES, 1915, is an immature *Halobia mousoni*, i.e. *Daonella mousoni* (MERIAN), according to NEWTON (1925).

The taxonomy of *Estheriella* is confused. Before RAYMOND's type designation (1946) of *Posidonia nodosocostata* GIEBEL for the genus, NEWTON (1910) cited *Posidonia wengensis* GIEBEL as its type species. This in turn was renamed *Estheria* (*Estheriella*) *costata* by WEISS (1875), because GIEBEL's (1857) is a homonym of *Posidonia wengensis* WISSMANN, 1841. *Estheriella* typified by *costata* is a distinct genus, instead of a subgenus of "*Estheria*". Its distinguishing characteristic is in the radial riblets strengthened in the medio-ventral part of the valve. Because they become weaker not only toward the umbo but also toward the anterior as well as the posterior side, it is difficult to count them exactly, but there are more than several and probably 20 or 30 at the maximum. The specific distinction is made by the radials and the outline of the carapace.

JONES (1891) considered *Estheriella nodosocostata* to be a synonym of *Estheriella lineata* WEISS. According to PICARD (1911) and also SCHMIDT (1928), they are quite different. While *lineata* is a typical

Estheriella, PICARD pointed out through his study on FRITSCH's (GIEBEL's original lost) in addition to fresh material that *nodosocostata* has 5 carinae regularly radiating from the umbo, beside some accessory radials. Because it is so different from *Estheriella* but similar to *Praeleaia*, CHERNYSHEV (1934) suggested *Praeleaia* for its generic reference. In my opinion it represents a new genus probably of the Leaiadidae, for which I propose *Mesoleaia*. It resembles *Leaia, Praeleaia* and *Metaleaia*, but disagrees with them in one or another characteristic.

Metaleaia is another intermediate genus between the Leaiadidae and the Estheriellidae. Like *Mesoleaia* it has 5 ribs which divide the valve into 6 sections of uniform breadth. The subdorsal section is narrower in *Mesoleaia*. In *Metaleaia triassiana* equidistant growth lines form a node at each junction not only with these ribs but also with the dorsal margin. The ribs become obsolete near the umbo. In *Praeleaia*, as in *Metaleaia*, 4 or 5 carinae radiate regularly and become obsolete near the umbo. There is, however, no distinct node on the ribs or on the dorsal margin and the carapace is longer and thicker in *Praeleaia*.

Nyasestheriella and *Congestheriella* are established respectively for *Estheriella nyasana* NENTON and *Estheriella lualabensis* LERICHE. Their description is, however, deferred to later pages.

As a distinguishing characteristic of Leaians RAYMOND emphasized the curious concavity in the interval between the radial carinae. The hollow nature of the carinae is another characteristic, as noted by JONES and others. The thickening of the dorsal margin and the limnadiform outline of the carapace are still other significant aspects sometimes seen in *Leaia*, but never seen in *Estheriella*. The radials inclusive of the dorsal one never exceed 5 in the Leaiadidae, but their disposition and curvature varies greatly. They are generally ridges or carinae, but in addition, a short radial groove is found in rare instances. These radial markings start always from the umbonal area, but some of them die out before reaching the ventral margin. The radials are of prime importance for taxonomy, but the ventral outline is also used for generic distinction by RAYMOND (1946).

Leaia is restricted here to the genus with an anterior and a posterior carina by which the valve is divided into three sections. *Eoleaia* is proposed for similar forms having two ribs, instead of two carinae.

Leaia quadriradiata which is the type species of *Quadrileaia* nov. has 2 secondary radials beside 2 primary ones. The secondaries are shorter and located close to the anterior and dorsal margins, but the margins themselves are not carinated. In *Leaia belmontensis*, the type of *Trileaia*, nov. there are 3 carinae aside from the dorsal one, which radiate from the adjacence of the umbo, dividing the valve into 4 sections with subequal umbonal angles.

RAYMOND classifies the Leaidians into *Leaia* and *Hemicycloleaia* mainly with reference to the ventral outline which is straight in the former and arcuate in the latter. The latter is, however, no more than a subgenus of the former, because there is every gradation. In the outline *Discoleaia*, nov. represented by *Leaia discoidea*, is quite isolated from other Leaian genera. It has a bicarinate subelliptical carapace.

In *Leaia* inclusive of *Hemicycloleaia* the posterior margin is sometimes recurved a little. But the limnadiform outline can never be seen and the dorsal carina is also absent in any unicarinate form. In RAYMOND'S *Monoleiolophus unicostatus* the radial ridge is not a typical carina as seen in *Leaia*, but a low round crested ridge. *Monoleiolophus* is a distinct genus, but it is more reasonable to group it with the Leaian genera than with the Estherians in view of the single keel tuberculate as in *Leaia* in LUTKEVICH'S *monocarinata*.

RAYMOND distinguished *Paraleaia* from *Leaia* by the narrow radial groove in the median section. *Paraleaia klieveri* is the type species which was formerly considered by GOLDENBERG (1877) and others to be possibly in the relation of sexual dimorphism with *Leaia beantschiana*, but this is difficult to determine. *Leaia intermedia* also has a secondary radial, but in the posterior section, instead of the anterior one. In *Leaia curta* which is the type species of *Bileaia* nov. two radials are disposed on the posterior side, and if one more carina is present, it is expected to be located close to the anterior margin. There is anyhow an unusually broad and non-carinate middle part.

Acantholeaia regoi ALMEIDA is a clear cut form. It is tricarinate. Two carinae run close to the dorsal and anterior margins and the dorsal margin itself is not carinate. The rest of the valve is divided by a postero-ventral carina into two sections of unequal breadth. This is a spiniferous Leaian and its spines are projected from a series of nodes on the subdorsal carina. The posterior outline is not lim-

nadiform.

Taxonomy is much easier in the case of Leaians and Estheriellians than in the case of Estherians, but if the proposed classification is to be natural, it is nevertheless not simple. Because the umbonal area reveals a juvenile stage in the carapace growth, the presence or absence of the radials in the umbonal area must be a more important criterion than the number and nature of the radials and their disposition. On the basis of this criterion, the Estheriellidae with smooth umbones and the Leaiadidae with those marked by radials, are primarily distinguished. Further notes on the genera of the two families will be found in later chapters.

CHAPTER II

Ecology and fossilization of the Conchostraca

1. Climatic control on the distribution of living Estherians

As a method of attack on ecological problems I carried out with the aid of KIDO (1943) a study on the distribution of living Estherians with reference to DADAY DE DEÉS' monograph. As to 101 species and 4 varieties of the Cyzicidae and Leptestheriidae, the temperature of their habitat and their distribution by latitude and longitude are cited except on 16 species of which the records are obscure.

Table II. Distribution of the genera of the Cyzicidae and Leptestheriidae

Genus	Specific Number	Latitude		Longitude		Isotherm	
Caenestheria	15	N S	28°–70°25′ 20°–32°	E W	26°–138° 96°30′–97°	N S	0°–24° 20°–24°
Caenestheriella	21 (2 vars. inclusive)	N S	10°–48°59′ 16°–44°	E W	6°–137° 2°–104°	N S	16°–30° 14°–24°
Cyzicus	18 (1 var. inclusive)	N S	15°–63°	E W	0°–130° 0°30′–128°	N S	2°–22°
Eocyzicus	10	N S	15°–37°36′ 32°–34°	E W	20°–77°5′ 18°–122°	N S	0°–28° 16°–26°
Leptestheria	16 (2 vars. inclusive)	N S	7°–51°30′ 3°–34°	E W	0°– 58° 4°–118°	N S	8°–30° 14°–26°
Leptestheriella	7	N S	5°–25° 3°–23°	E W	2°– 81°	N S	24°–28° 22°–26°
Eoleptestheria	3	N S	28°–48°	E W	27°–130°	N S	0°– 2°

While the distribution of *Eoleptestheria* is very limited, *Caenestheria* spreads most extensively, as shown in Table II. Because the latter occurs from the tropical to the frigid zone, it is eurythermal. The former on the contrary must be a stenothermal genus, seeing that its distribution is expanded latitudinally rather than longitudinally in the temparate zone of the northern hemisphere.

Incidentally it is easy to see that the smaller the number of species in a genus, the more limited its distribution. *Eoleptestheria* is possibly a case in point. It is a small genus. But the number does not always correspond to the distribution of a genus. For instance, *Cyzicus* comprises more species than does *Caenestheria*, but the former is more

confined in its distribution than the latter. This is because many species of *Cyzicus* are found crowded in a limited area, probably due to the higher variability and stronger stenopic nature of *Cyzicus* than *Caenestheria*. I examined the distribution of various species in the seven genera in further detail and found that they may be aligned from stenopic to eurypic as follows:

(1) Among 18 species of *Cyzicus*, 14 species, that is 77 percent, are found in E. 0°–40° and N. 30°–50°.

(2) *Eoleptestheria* is a small genus occurring within the limits of E. 25°–130° and N. 30°–50°.

(3) In *Leptestheriella* 5 species are African and 2 Indian.

(4) *Leptestheria* comprises 7 African, 5 European and 4 American species and their distribution in each continent is quite restricted.

(5) In *Eocyzicus* there are 5 Asiatic, 3 African and 2 American species which occur in places widely apart from one another on these continents.

(6) *Caenestheriella* in 19 species are widely distributed without much regard to longitude and latitude, namely E. 0°–150° and N. 50°–S. 45°.

(7) *Caenestheria* represents a typical example of discontinuous distribution. Out of 14 species 5 are living in Asia, 4 in northern tundra, 3 in Australia, 2 in Africa and 1 in North America.

In *Leptestheria* 50 percent of the species or 8 of 16 species are spread widely. *Caenestheria* is the next in which 35 percent or 5 out of 14 species are extensively distributed. In *Cyzicus* on the other hand the widely distributed species comprise 14 out of 18 species or 78 percent.

The distribution of Estherian species is mostly not very extensive. *Caenestheriella ehrenbergi* whose distribution extends from N. 23° to S. 23° and from E. 30° to 130° is an exception, but the Australian one from Yalgov is distinguished from the Egyptian one as var. *michaelseni*.

The distribution of living Estherians is intimately related to the isotherm in the hot season, or more precisely, in July in the northern hemisphere and in January in the southern hemisphere, as shown in Figure 8. In fact all of them except *Caenestheria skorikowi* of Archangelsk region are between the isotherms of 10 degrees C. Most of them are between the isotherms of 20 degrees C, if 4 species of *Caenestheria* and 2 species of *Cyzicus* are excluded. *The specific numbers of Estherians*

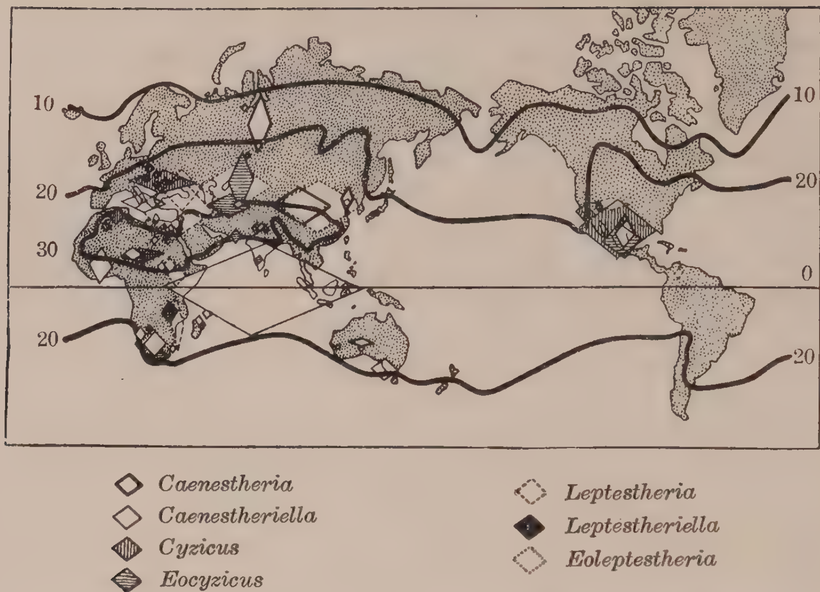


Figure 8. Distribution of genera of the Cyzicidae and Leptestheriidae.

are, however, larger in the warm temperate zone of 20° to 30°C. in hot seasons than in the tropical zone above 30°C. Because Estherians are fresh water inhabitants, the climatic difference evidently refers to water temperature. The circum-Mediterranean region is the center of distribution. The greatest variety of species is found in inland basins, especially of the middle Donau river, the Nile and the great rift valley of East Africa, the fact suggesting that *a continental climate is more favourable than the oceanic one for this kind of creature.*

In this connection it is noteworthy that *Caenestheriella gifuensis* from Yamada and Koriyama respectively in the inland basins of Omi and Nara is exclusively larger than the species from Tomoroki in the coastal plain east of the Osaka bay. (See KOBAYASHI and KUSUMI, 1953, fig. 7).

2. Glacial control on the distribution of living Estherians

As discussed above, the climate or water temperature in hot seasons seems to be the most important factor controlling Estherian distribution. If so, the ice cap in the interior of the Eurasiatic continent in the Diluvium must have been a great barrier.

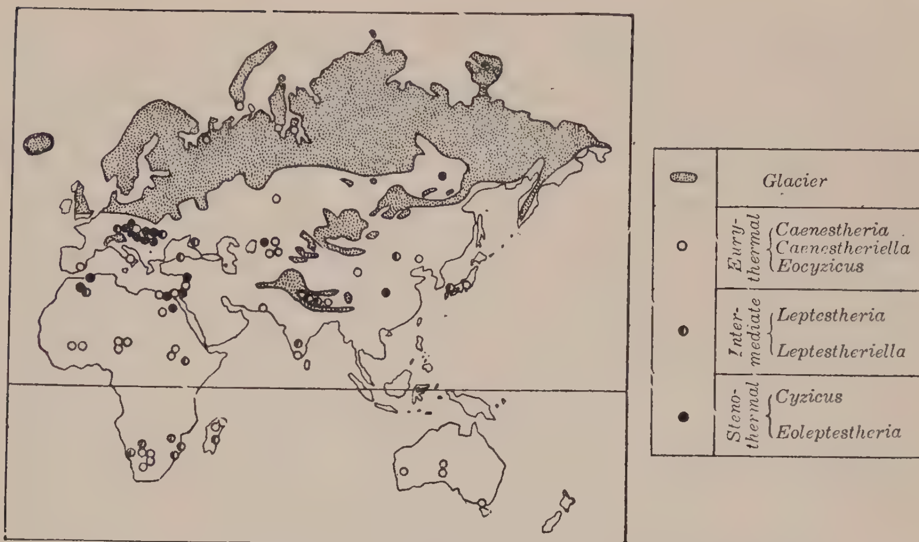


Figure 9. The glaciation of the Diluvium and the present distribution of the genera of the Cyzicidae and Leptestheriidae.

Among 12 species of which I am aware from Eastern Asia, 6 species, 3 in each, belong to the most eurythermal *Caenestheria* and *Caenestheriella*, 2 to *Eocyzicus* which is also fairly eurythermal and 4 species, 2 in each, belong to intermediate *Leptestheria* and *Leptestheriella*. Stenothermal *Cyzicus* and *Eoleptestheria* on the other hand are represented by 2 species, 1 in each.

It is an interpretation that, interferred with by the ice cap on the Ferghana-Sayan uplifted zone in the near past, the dispersal from the center of the distribution area in the circum-Mediterranean region was not so easy for stenothermal Estherians as for eurythermal ones.

3. Discontinuous distribution of fossil Conchostracans

Cosmopolitan species are common in the Cladocera. In the Anostraca and Notostraca there is a general tendency to increase the number of their species and genera toward the equator. As discussed already the Conchostracans are, however, thriving less in the tropical than in the subtropical zone. Inland basins in the warm temperate zone provide the most favourable environment where Estherians flourish. Due to endemism many living Estherians are local species. Oceans evidently constitute the greatest barrier not only for Estherians but

also for most other limnobios and geobios. The trans-oceanic distribution of fossil Conchostracans is therefore an important problem.

Leaia leidyi inclusive of 4 varieties *salteriana, williamsoniana, baentschiana* and *klieveri* used to be the most widely spread species among Leaians. Their occurrences are reported from the Carboniferous formations from eastern North America, Great Britain, France, Germany and Iberia (TEIXEIRA, 1950). The trans-oceanic distribution of the Mauch Chunk species into Europe is, however, hard to accept for modern students. RAYMOND who apparently does not like varieties (1946, p. 249), distinguished 9 species and 3 genera in *leidyi*. It is, however, a question whether there is no variety relation among the forms in the same province in Europe or North America. In the case of same age or province morphic variation should be examined very carefully to see whether it is continuous or discontinuous. Warning is provided by my observation on *Euestheria middendorfii* (KOBAYASHI and KUSUMI, 1953). Its distribution is extensive and continuous. Morphic variation among many forms of the species is also continuous where a large number of specimens are examined.

Estheria mangaliensis has been a cosmopolitan. It was first described from peninsular India, but later reported to occur in Australia, Africa, North and South America. Its distribution is thus much wider than that of *Caenestheriella ehrenbergi*. MITCHELL correctly gave a new name, *ipsviciensis*, for the Australian form. Var. *angolensis* and var. *pennsylvanicus* are perhaps distinct species in each. The Rhaetic one of Mendoza in Argentina is still another species, *forbesii*.

Estheria minuta is another cosmopolitan reported from Europe, the Urals, Siberia, Indochina, New Zealand, Africa and North America. According to RAYMOND (1946) *Estheria minuta* from the Permian of Kansas belongs probably to his *Lioestheria raaschi*. He is right in erecting *autunensis* for the Permian form of *minuta* in France. Upper Permian *Euestheria* cfr. *minuta* from Africa (MARLIÈRE, 1950) may also be a new species.

RAYMOND recongnized *Estheria minuta karpinskiana* from the Rhaetic shaly marl of Troizk, near Tschelabisk in the Eastern Urals as a distinct species probably of *Bairdestheria*. *Estheria minuta* of the Kuznetsk basin in Siberia looks somewhat similar to *Lioestheria aequale* in the outline of the carapace, punctation and the number of growth lines. Because its test is punctated, instead of polygonally reticulated as in true *minuta* (LUTKEVICH, 1937), I wish to call it *Lioestheria*

pseudominuta, new species. *Estheria subcircularis* CHERNYSHEV is also based on another form of the so-called *Estheria minuta* in the Kuznetsk basin. Although nothing is mentioned of the test, Indochinese *minuta* can readily be distinguished from the European one by the outline dilating posteriorly, instead of anteriorly as in true *minuta.* Therefore a new name, *Euestheria mansuyi,* is proposed for it. The holotype is the left valve in fig. 3 a on pl. 10 in MANSUY (1912).

Recently BOCK (1946) claimed that LEA's *ovata* and EMMON's *multicostata* from the Newark series belong to *Estheria minuta* itself, but this *minuta* was later assigned to *ovata* by him (1953). The so-called *minuta* from the High Atlas which has small polygons as its sculpture, must be an *Euestheria* as suggested by DEFRETIN and FAUVELT (1951), but their illustration does not show the anteal dilation of the carapace outline. An Estherian procured from the upper Wairoa series (Triassic) of Nelson, New Zealand, is identified with *E. minuta* (CHAPMAN, 1914), but it may be a juvenile *Halobia* according to FLEMING. (See page 110).

These species provide some remarkable examples of discontinuous distribution. Reexaminations enabled me to split them into some species or even into genera. The discontinuous distribution of small genera is also another interesting subject for study.

Estheriella as defined in the preceding page is restricted in its occurrence to the Buntsandstein. The so-called Carboniferous Estheriellians belong to *Anomalonema.* KROTOW's *Estheriella* and *Estheria* from the Permian of the Urals (1888) are, according to LUTKEVICH (1941), calcareous shells of pelecypods. Therefore there is no linking form between *Anomalonema* and *Estheriella* in Europe.

Estheriellians are, however, not less developed in Africa than in Europe, but at the same time African ones, or at least most of them, may belong to genera different from true *Estheriella. Estheriella nyasana* from the Karroo in East Africa has radials typical of "*Estheriella*" (NEWTON, 1910), but the outline of the carapace is so different from German *Estheriella,* that it is distinguished as *Nyasestheriella.* In view of the strongly nodose radials and the strong convexity and ovate outline of the carapace, *Estheriella lualabensis* can be generically distinguished from German *Estheriella* as *Congestheriella.* "*Estheriella*" *bornhardti* also disagrees with *Estheriella* s.str. in the elliptical outline, stronger convexity and mode of ornamentation. *Estheriella moutai* may be the nearest to the Buntsandstein

forms, but its radial ribs are stronger than in them.

Estheriina presents another example of discontinuous distribution geologically as well as geographically. The genus was established by JONES on the basis of a Bahian or Neocomian species of Brazil. But he referred *Estheria limbata* and *Cardinia freysteini* from the Carboniferous of Germany to the genus. Ladino-Carnic *Estheriina atsuensis* and *E. nakazawai* have similiar umbonal swells. These species closely resemble *Estheriina linguiformis*. Judging from their distribution it is quite reasonable to consider that the swells have appeared in some branches from the Estherian stock at several times in different provinces. *Estheriina* are evidently polyphyletic, but it is very difficult to classify these species on a phylogenetical basis.

In the case of Neocomian *Pseudoleaia*, however, it is not only isolated from the Leaians but also differ in the mode of radial marking. Therefore the conclusion is warranted that *Pseudoleaia* is a terminal form of the Lioestheriinae. This is good evidence which supports the view that Conchostracans with radials branched off more than once from the Conchostracans without radials.

4. The relations of the carapace size and number of growth lines to climatic condition

Caenestheria is the most eurythermal of the 7 genera. In this genus 4 species are known far north in the tundra. They are all relatively small in size, namely 5.5–12.2 mm. in height and 3.5–8 mm. in length, although they are not the most diminutive in the genus. In the Donau basin where the climate is the optimum for the Estherian, the carapace becomes larger, or more precisely, 8.4–15 mm. in height and 6–11 mm. in length in 4 species of *Cyzicus* and 7.8–20 mm. in height and 5.3–13 mm. in length in 3 species of *Eoleptestheria*. The size of the carapace varies greatly in *Cyzicus* and *Eoleptestheria* in the temperate zone. The variation of growth lines is much greater in *Eocyzicus*, while they are about 20 in *Caenestheria* on an average.

There may be of course multiple factors in the increase of carapace dimension. The climate or water temperature in hot seasons, however, appears to be the factor of prime importance. If the climate is unfavourably cold for the Estherians, their carapace is small and has only a small number of growth lines. Although the number of growth lines is less significant than the carapace size, it appears to be a

general tendency for the number to attain its maximum in the stenopic forms in which the variation of the carapace size is also wide.

In connection with palaeoclimatology, especially interesting are two Estherian faunas from the Nordwick-Chatanga region in Siberia. They are faunas fairly rich in the most northern region, although a solitary species is known from Spitzbergen. The dimensions of the carapace given by NOVOZHILOV are plotted and shown in figure 10.

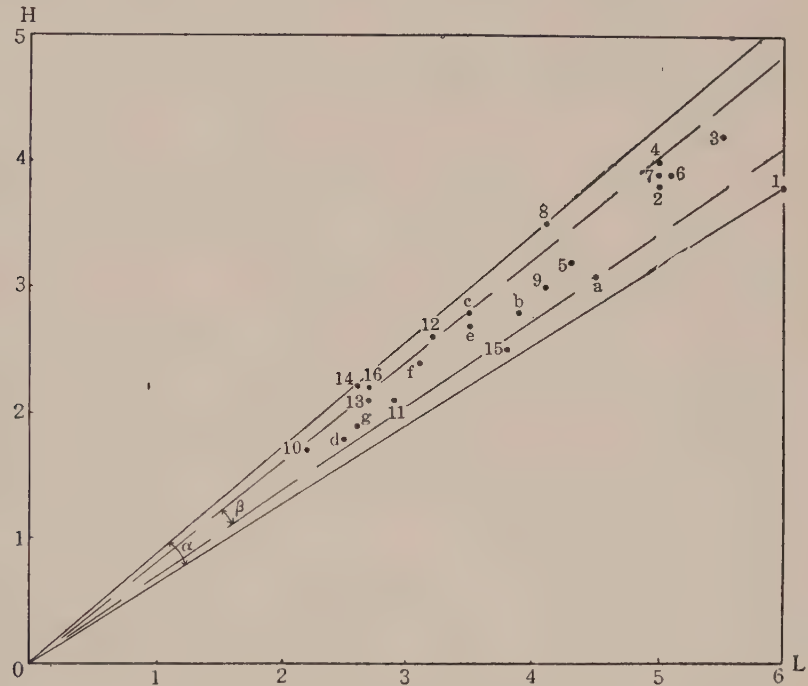


Figure 10. Height-length proportion of the Permian and Triassic Estherians in Northern Siberia. See page 101, for Nos. 1-16, (Permian Estherians) and page 102 for a-g, (Lower Triassic Estherians).

The Permian fauna of the region comprising 15 species and 1 variety are exclusively small. The longest is *Euestheria chatangensis*, 6 mm. long and 3.8 mm. high and the highest is *Euestheria strictocostata*, 5.5 mm. long and 4.2 mm. high. Growth lines attain 30 in *Euestheria multinstita*, but less than 20 in all others.

The Triassic Estherians of the same region are still more diminutive. Among 7 species the largest is *Lioestheria tigjanensis*, 4.5 mm. long and 3.1 mm. high. There are 17 growth lines in *Estherites*

deverta, but the number of the lines is between 5 to 10 in the remaining species.

As can be expected from the high latitude, the habitat may have been unfavourable for the Estherians. It was especially so in the early Triassic period, as indicated by the diminutive forms.

5. Mesozoic climate in Eastern Asia judged by the Estherians

Among the Mesozoic Estherians in Eastern Asia, their size varies, as summarized below:

(1) The Estherians in the Daido fauna are all small except one which is fairly large.

(2) Those of the Jehol fauna are large to medium in size, including the largest so far known.

(3) The Estherians in the Kyöngsang fauna are medium-sized and growth lines are numerous in many of them.

(4) The Sungari Estherians are a little smaller than the Kyöngsang in size, and growth lines are generally not so numerous.

Therefore climatic condition must have been best for the Estherians in the Jehol epoch and worst in the Daido epoch, insofar as the size of the carapace is concerned. The Kyöngsang and Sungari epochs were intermediate. If the number of growth lines is taken into account, the Kyöngsang Estherians may be more stenothermal and the Sungari Estherians more eurythermal. If compared with the above-mentioned Siberian faunas, the Estherians of the Jehol fauna are gigantic, the carapace, three times longer or higher than the maximum length or height of the Permian ones in the Nordwick-Chantanga region being not uncommon in the Jehol fauna. The optimum condition for the Estherians which prevailed in Eastern Asia in the Jehol epoch will be discussed later from other points of view. (See page 80.)

6. Mode of life and carapace growth

Recent Estherians are living mostly in fresh water and rarely in brackish water. In Japan they are found in shallow pools in May, June and rarely in July and most commonly in the shallow waters of rice fields in the provinces of Mino, Omi, Yamato, Kawachi, Aki and so forth, all located in the median part of West Japan. I have not heard of any occurrence in the coastal region either on the Pacific side

or on the side of the Japan sea or in North Japan. In Manchuria and Mongolia they are found in the shallow waters of ponds and palyas. They are mud-eaters and, in crawling into mud, take minor organisms in detritus. When swimming, they drive their second antennae back and forth.

As usual in the Euphyllopoda, they pass the nauplius stage after hatching from the eggs and repeat moultings before sexual maturity, but the number of moultings varies according to nutrition, temperature and other factors. *Limnadia lenticularis* has in the older larval stage a narrow dorsal shield protruded back into a long spine. In the young in the post-larval stage, the shield is sinuated at the rear like that of *Apus*, but the anterior outline is also carved backward (SARS, 1896). Because the shield in these stages is a single plate, bivalves are possibly introduced secondarily by folding.

Like in *Apus*, the ecdysial suture of *Lynceus* runs along the periphery of the valve, but it extends to the rear part of the valve, instead of terminating at the postero-lateral angles of the sinuation in *Apus*. In the front the line runs behind the eyes. In *Limnadia* and allied genera the suture runs similarly all along the periphery of the carapace, but "*the dorsal leaf of the old cuticle is not cast off, but remains in position, giving rise to a series of lines of growth on the shell, just as in a lamellibranchiate Mollusca*" (HENRIKSEN, 1932, p. 106).

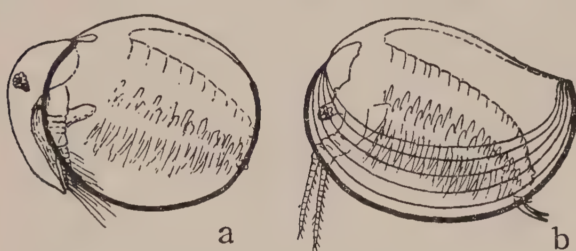


Figure 11. Ecdysial sutures of *Lynceus* (a) and *Limnadia* (b) (ater HENRIKSEN).

According to BERRY's observation (1926) on *Eulimnadia storingtonensis* its life cycle is 23 days. The incipient valves, 1 mm. long, appeared on the third day after hatching and 8 growth lines could be counted on the carapace, 5 mm. long, on the ninth day but only one growth band was added by the sixteenth day.

Incidentally the breadth of the interspace between growth lines does not increase regularly. In *Euestheria middendorfii*, for example, the growth bands in the middle stage are wider than those before and after. A few lines near the periphery are sometimes close-set with irregular interspaces. This aspect reveals senility. In a very rare

instance one or two growth bands become broader again in the most peripheral zone, the aspect being suggestive of rejuvenescence in the senile stage.

It is interesting to see in *Estheria malangensis* (MARLIÈRE, 1950) that the juvenile carapace of the species having subcentral umbo on the high ovate carapace becomes a broad carapace with a terminal umbo in maturity. In the morphic series he illustrated, however, there is some gap between the d and e forms. A question is also attached to the growth lines of the f form which are all parallel to the periphery of the carapace and do not show morphic change through growth. Nevertheless this is a line of research very important for Conchostracan palaeontology.

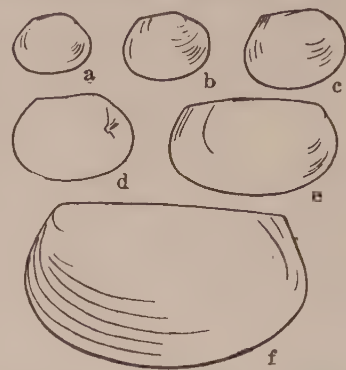


Figure 12. Change of the carapace outline of *Euestheria malangensis* (after MARLIÈRE).

Although little is known of the mode of copulation, reproduction generally takes place in the Conchostraca sexually, instead of by parthenogenesis. Eggs are kept in the postero-dorsal part of the female in the valves before they become free. They pass the cold season in egg capsules. As demonstrated by SARS and others the eggs of the Conchostraca or Euphyllopoda in general are extraordinarily durable under severe conditions. They can hatch in water after 3 or 5 years.

In a test an egg kept dry for several years was hatched (SPANDL, 1925). Therefore Estherian eggs shielded in capsules are quite safe, unless they are dried up or frozen to death by unusually high or low temperatures.

7. Egg-capsules and their dispersal

I have already mentioned the eggs of *Lynceus stchukini* which are found in the postero-dorsal part. JONES reported the occurrence of egg capsules in association with carapaces of *Euestheria middendorfii* in Transbaikalia, one of which reveals regular trifurcate clefts.

Similar sphaerules are occasionally met with in shales of the Cretaceous Sungari series in Manchuria. Their diameter measured on the bedding plane is about 0.25 mm. The sphaeric body is somewhat flattened. A few of them are empty but most others are filled up

with dirt. The surface is smooth and frequently coated by a film of iron oxide. Purplish minute grains are sometimes seen in the hollow. They are vivianite according to Dr. T. SUDO's test. These sphaerules are all found together with Estherians except in the case of a bore-core from Tiehli, in North Manchuria.

Judging from their minute size and frequent association with Estherians which attain in their largest species *Estherites mitsuishii* a length of 9 mm. and a height of 6.5 mm., it is probable that the sphaerules are Estherian egg capsules. Ostracodes are also common associates, but the sphaerules are too large to be their eggs, because even the largest *Candona gigantea* (HANAI, 1951) is only 2.5 mm. in length.

At my request Dr. UENO kindly gave me some specimens of recent Estherians. The carapace of *Caenestheriella gifuensis* is about 8.5 mm. long and its eggs are 0.25 mm. or a little less in diameter. The eggs of the two female specimens of *Caenestheria davidi* vary in diameter from 0.23 mm. to 0.19 mm., and to which diameter a narrow brim of 0.02 mm. should be added on each side. These carapaces are about 11.7 mm. long. The sphaerules in question are not much different from the eggs of the two species in size.

Figure 13. Egg-capsules of *Limnadia lenticularis* (After DADAY DE DEÉS).

Assuming that they are Estherian eggs, it is inferred that impure water containing iron and phosphate flowed into the capsules through the clefts and ferruginous minerals deposited therein. The presence of vivianite is a proof of the lacustrine origin of the Sungari series.

Like the seeds of some anemophilous flowers, the eggs of *Limnadia lenticularis* has a well developed brim. It is somewhat different from any of the Cyzicidae and Leptestheriidae. Eggs of 36 forms of these two families which DADAY DE DEÉS illustrated can be classified into eleven types, as illustrated in figures 13 and 14. But there is no generic speciality as can be recognized from table III. Furthermore the fossil eggs above-mentioned are all simple, smooth spheric bodies.

Fossil eggs remain to this day no more than a curiosity. But the bearing of the eggs on the dispersal is very important. Because the eggs provided with brims are easily blown about, wide dispersal of Estherians from a basin to another must have been due principally to

wind. As discussed already, climatic influence is strong on the Estherians. Therefore the transported eggs may not all hatch or grow up. But some of them would become indigenous or even flourish suddenly if the new habitat were suitable. Such a mode of dispersal enables the geologist, on the basis of limnobios, to correlate formations beyond the bounds of a single basin or a hydrographic province.

Like meroplanktonic transportation for halobios, wind carriage of egg-capsules is thus a very important factor in the dispersal of Estherians. My attention is diverted in this connection to the volcanic eruption of Krakatua in 1883, which completely destroyed all forms of life on the island. TREUB of the Buitenzorg museum visited the island in 1886 and found there many blue green algae, 11 species of ferns, 39 flowering plants on the beach and 8 flowering plants in the interior. Most of their spores or seeds are presumed to have

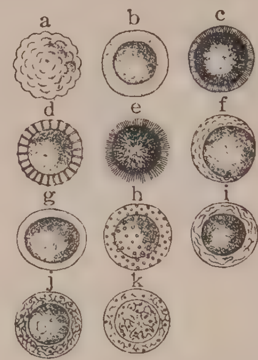


Fig. 14. Egg-capsules of the Cyzicidae and Leptestheriidae. (See Table III for the names of these types).

Table III. The number of forms of the Estherian genera having different types of eggs.

Type of eggs	Genus	*Caenestheria*	*Caenestheriella*	*Cyzicus*	*Eocyzicus*	*Leptestheriella*
a	*sibirica*	4	2			
b	*davidi*	1				
c	*sahlbergi*	2	3	1		
d	*berfragei*	1	1			
e	*educta*		2	9		
f	*rubra*		2			
g	*joubini*		2			
h	*crinita*		2			
i	*consors*			1	1	
j	*villigera*					1
k	*aethiopica*					1
number of described forms		16	22	27	11	7
number of forms with illustration of eggs		8	14	11	1	2

been brought to the isle by wind or sea-current. By 1897 50 species of flowering plants were found and small clusters of forests had already come into existence. The flora of Krakatua at the time was, however, infinitesimally less than the 5000 species known in Java. At the same time it should not be overlooked that a quarter of a century is an extremely short span of time in comparison with a geological age. The dispersal of Estherians or Leaians over the Tethyan sea must have been by the carriage of egg-capsules by wind.

8. Biocoenosis and thanatocoenosis

As mentioned already, the ratio of males to females in the recent Estherian species differs according to environment. The ratio may differ still more between a bio- and a thanatocoenosis. Fossil Estherians may be found far from their habitat, because a carapace becomes nekroplanktonic if an air-bubble gets in between its two valves. As the valves are light, they can easily be blown by wind for a long distance. I was told that in Manchuria Estherian carapaces blown by wind are found on the shores of pools or even in large water-jars. This is another reason why the same Estherians occur in formations in isolated basins.

Seeing that the main habitats of living Estherians are small shallow pools, it is a question whether fossil Estherians in extensive lacustrine sediments lived in the lake where the sediments were accumulated. It is not improbable that many Estherians are exotic elements in a fossil-coenosis. There is, however, a fact which shows that Estherian habitats are not always remote from their burial places. It is found sometimes that many Estherian carapaces are not dismembered. Though less commonly the two valves of a carapace are sometimes open but still fused, as illustrated in fig. 6, on pl. 1, (KOBAYASHI and HUZITA, 1942). In such a case it is evident that the burial place is not far from the habitat, because the two valves without hinge teeth or ligaments easily separate from each other.

A specimen of *Euestheria* aff. *amurensis* (KOBAYASHI and HUZITA, 1942, pl. 2, figs. 3) shows that the two valves are displaced by water current more widely on the anti-umbonal than on the umbonal side, because the attachment is still maintained near the umbo. A weak current in a fossil lake is better illustrated by similar displacement

between the two valves which is in the same direction in many pairs of valves on a slab from the Jehol group (KOBAYASHI and KUSUMI, 1953, text-fig. 2). Because these carapaces must have been entombed in the sediment before the complete decay of the body, these fossil localities can not be very far from Estherian habitats.

As described in detail on a previous occasion (KOBAYASHI and HUZITA, 1942) a specimen from the Sungari station presents an interesting example of a removal of the carapace. In slabs of gray shale many detached carapaces are found crowded together densely within the sharp boundary between the light colored, coarser band below and the dark colored, finer band above. There is, however, none in the upper band but some are found scattered in the lower band. Their number, however, decreases downward while the shale becomes darker and finer. My interpretation is that the boundary indicates a transition from wet to dry season when Estherian carapaces were transported by torrential floods and settled on the bedding plane. Insofar as Estherians are concerned, a thanatocoenosis is sometimes quite different from a biocoenosis. Estherians occur not only in fresh water facies but also in brackish facies where most, if not all, are exotic members.

9. Estherians in limnic and paralic facies

Fossil Estherians occur in Eastern Asia most commonly in varicolored lacustrine formations. The colors may be yellowish, reddish, greenish or greyish and rocks are generally fine-grained. The specimens from the Jehol group provide typical variegated examples some of which are fairly coarse or tuffaceous. Estherians are sometimes found in association with lycopterids (TAKAI, 1943), *Astracus* (IMAIZUMI, 1938) and other limnic inhabitants. Some specimens from the Sungari series contain many non-marine ostracodes (HANAI, 1951) beside Estherians.

In the Carboniferous coal measures of Europe Estherians are frequently accompanied by naiads, but such coexistence is rather uncommon in the Mesozoic in Eastern Asia, notwithstanding the fact that there was a rich naiad fauna, as summarized by SUZUKI (1949). In the Daido group Estherians are frequently contained in black carbonaceous shales. The specimen from the formation in the Rampo area in Korea is a plant bearing shale. In the Asa area, Prov. Nagato (Yamaguchi Pref.), the lower Carnic Estherian shale is located between the coal measures of Tsubuta and Akaiwa. The specimen from Hei-

tingshan in the middle part of the Great Khingan range is mudstone. The Estherian bands in Wurtemberg in Germany is located in gypsiferous mudstone of the Keuper (FRECH, 1903–08).

These are all lacustrine sediments. Estherians are especially abundant in paper shales. The Cretaceous oil shale in Chientao, Southeast Manchuria, is such an example. Estherian carapaces on the very finely laminated fossiliferous shale glisten with brownish or greenish gray colour.

Lynceus (*Limnetis*) *stchukini* in unusually good preservation is considered to have been buried under quite a shallow stagnant body of water which did not dry up periodically. Dark or even black and exceedingly fine-grained shale provided favourable environment for the preservation of the soft part. Cretaceous climate of Transbaikalia at that time is comparable to that of Ukraina today (CHERNYSHEV, 1940). For the Estherian beds of the Nordwick-Chantanga region a deltic condition in a closed basin isolated in North Siberia is suggested by NOVOZHILOV (1946).

Because the dispersal of the carapace is so easy and so wide, Estherians happen to occur in paralic facies of sediments. In Japan *Pseudoleaia rectangula* (YOKOYAMA) is known from a Lower Cretaceous paralic sediment in the Yuasa basin in Province Kii. Estherians from Hikiji, in Prov. Nagato, are contained in light yellow or purplish clayey rock which is not well consolidated. The Mine series containing Estherians is a paralic formation.

In Tonkin, Indochina, *Lioestheria mansuyi* occurs in limestone containing *Gervilleia alloucheryi* and *G. haloensis*. Near Tübingen in Germany, *Euestheria minuta* is found together with *Lingula tenuissima*, *Trigonia goldfussi*, *Gervilleia socialis* and fishes in dolomitic limestone at the top of the Lettenkohle where these pelecypods reveal a dwarfing (QUENSTEDT, 1843). Similarly *E. minuta* is reported to occur together with *Lingula tenuissima* in marl and dolomite in alternation in the upper Keuper in the lower Rhein (DAUBRÉE, 1852). In Livonia *Lingula*, *Asmussia* and others occur in the Old Red Sandstone.

MAUZ's *Paracyclas rugosa* (1933), i.e. *Lioestheria diensti* occurs in the Lower Devonian of Eifel in Germany with marine ostracodes, Molluscan shells, Gigantostraca and fishes (GROSS, 1934). In the Lower Devonian of Ardenne in Belgium *Euestheria stockmansi* is found associated with *Spirorbis* (MAILLIEUX, 1933). In Harz *Quadriasmussia herecynica* was obtained from the Kulm containing marine ostracodes,

trilobites, brachiopods, crinoids and stegocephalians (KUMMEROW, 1939). Is it improbable that Estherians lived in a shallow sea at the beginning?

Thus Estherians are contained in various kinds of rocks. In New South Wales Estherians occur in Upper Permian cherty tuff which yields also insects and other fossils (MITCHELL, 1927). Leaians are procured in a clay-ironstone nodule with coprolites, fishes, plants and others in the Lower Carboniferous shales of Wardie, near Edingburgh (JONES, 1871). MEEK and WORTHEN's holotype of *Leaia tricarinata* is preserved in a pyrite nodule. I have not, however, read or heard of any contained in very coarse sandstone or conglomerate. There is no record of their occurrence in bathyal sediments. Estherians are, however, not restricted to limnic facies but occur also in paralic or even neritic facies. Therefore they can be the key to stratigraphic correlation among heteropic facies.

Finally the reddish gray Estherian shale of Termini, Prov. Palermo, in Sicily, is inserted into the marine *Halobia* limestone. Insofar as I can see in SALINA's strongly magnified illustration ($\times 540$), the textures of *Estheria ciofaloi*, *E. radiata*, *E. ameliae* and also *E. gemmellaroi* and *E. schofenii* look dissimilar to the granulation on the Estherian carapace. The granules are more likely minute crystals of calcite or aragonite of Molluscan shells. The radial markings of *Estheria radiata* and its variety *oblongata* are strongly suggestive of the Halobidae. GEMMELLARO's *Halobia radiata* also from the Carnnic *Halobia* limestone of Sicily is placed in *Halobia* (KITTL. 1912, DIENER, 1925). Therefore I cannot be convinced that the intercalating bed is really an Estherian shale.

10. Fossilization and deformation

Estherian carapace is thin, chitinous and flexible. Therefore the modes of fossilization and defossilization are different among Estherians, ostracodes and pelecypods. Although statements on this point are rare, I found a reference in an old report to a remarkable example of differential fossilization. GÜMBEL (1865) noted in material from Thüringener Wald that "*Estheria*" *rugosa* was found in association with *Unio* and *Anodonta* where the naiad-shells are mostly replaced by iron-pyrite and partly by zincblende, galena or calcite, but not the Estherian carapaces.

Estherians in paper shales are generally well preserved. Some of them in the Chientao specimen are altered by pyritization. In the calcareous sandstone from Shangyuan in Jehol, the carapaces of *E. middendorfii* var. *jeholensis* and its var. *elongata* are calcified, and their sculpture is unusually well preserved. The defossilization depends upon circulating water and accordingly the porosity of rock but at the same time the chemical composition of the water and fossils are other important factors. Differential defossilization between Estherians and other fossils is a subject as yet little studied.

In many Estherians I have seen, sculptures are better preserved in the interspaces near the periphery than in other parts. When carapace-valves are secondarily wrinkled, it is difficult to see their aspect. It is especially difficult to count growth lines exactly. In *E. middendorfii* it is easy to miscount one or two, sometimes three, more or less growth lines. Two kinds of concentric lines or ridges are sometimes met with, one being stronger and well impressed even on the internal mould, but the other can be seen only on the outer surface of the carapace. The two kinds are, however, not always distinguishable from their external view.

Carapace-valves are inflated in the marl of Heitingshan, but they are frequently flattened by diagenetic pressure during compaction. The secondary flattening of the carapace differs according to original convexity. *E. atsuensis* from Prov. Nagato has a convex umbonal area which is mostly crushed by depression but not the flat part. It can easily be imagined that the outline would be deformed more when valves lie oblique to the bedding plane than when parallel to the plane. When an Estherian bed is deformed, carapaces in the bed are naturally deformed. These primary and secondary deformations make their identification very difficult.

Estherian fossils may vary in outline to a great extent at one locality but not so much at another, notwithstanding the fact that they are contained in the same formation. In such a case it is highly probable that this morphic diversity depends largely on later deformations. Individual variation, however, can be original. Sexual dimorphism and endemic polymorphism must be brought into consideration. Unless the least deformed and well preserved specimens are selected, specific concept can be quite misleading.

11. Conchostracans as index fossils

The dispersal of Estherian eggs by wind, drifting of the carapaces of dead Estherians and their wind carriage help the correlating of formations in heteropic facies or in different hydrographic provinces. Estherians occur in various formations widely in Eastern Asia, and are especially abundant in certain Mesozoic sediments. This is why I have taken up Estherians for study.

In the course of my study, however, I was faced with great difficulty because of the insignificance of the features of Estherian carapaces. The features are the outline of the carapace, position and shape of the umbo, the number of growth lines and the mode of sculpture in their interspaces. The outline is variable within a species, partly due to secondary deformation, and accordingly it is not simple to estimate the true height-length proportion. The umbo also is difficult to locate exactly when it is obtuse. As discussed later, localization is strong in some kind of Estherian fauna. In another kind the same fauna is distributed very extensively, but at the same time polymorphism within a species is great. These reasons make it difficult to grasp the specific concept. This difficulty in specific identification is a disadvantage in using Estherians as guide fossils.

Because Estherians are indigenous, intercontinental correlation on their basis may be unreliable, but they can be used as time indices within the bounds of their local or regional distribution. When so confined, it becomes easier also to find out the morphic significances of each species.

In the Triassic system of the German facies *Estheriella* s. str. is a characteristic genus in the Buntsandstein. *Euestheria minuta* is widely distributed in the Lettenkohle. It occurs in Great Britain too. Var. *brodieana* in the Rhaetic of Scotland and England indicates mutation from *minuta* in its smaller polygons in the interspace. This variety is reported from Schilesia in Germany. *Euestheria laxitecta* marks off a zone in the lower Gypskeuper in Franconia (THÜRACH, 1890) and is

Table IV. The *Euestheria laxitecta* stage in the Keuper (THÜRACH).

III. Stufe der *Estheria laxitecta* SANDB.	3. Obere Gypsmergel und obere Estherienschichten; 8–19 m.
	2. Mittlere Estherienschichten; 20–40 m.
	1. Untere Estherien und *Corbula* Bänke; 3–7 m.
II. Stufe der *Myophoria raibiana*.	
I. Stufe der *Myophoria goldfussi* od. Grundgypsschicht.	

traceable into Alsace as well as into Coburg and Lorez. The base of the Triassic in New South Wales is drawn by the Estherian shale. When the sediments lack any other guide fossil, Estherians help geologists.

Table V. Zonation of the Carboniferous formation in the Donetz basin by means of Naiads and Conchostracans (after CHERNYSHEV).

Fossil zone	Donetz basin.	Age
7° *Anthracomya jakowlewi, Leaia baentschiana, Estheria ortoni*	C_3^{2+3}	Stephanian inférieur
6° *Estheria cebenensis, Anthracomya pruvosti*	C_3^1	Westphalian D
5° *Estheria simoni*	C_2^{5+6}	Westphalian C
4° *Anthracomya pulchura*	C_2^{4+5}	Westphalian B
3° *Anthracomya williamsoni, Carbonicola rhomboidalis*		
2° *Carbonicola ovalis, Carbonicola turgida*	C_2^{2+3+4}	Westphalian A
1° *Carbonicola robusta, Carbonicola janischewskii*		(Assie Vicoigne)

As shown in table V, CHERNYSHEV (1931) classified the upper Carboniferous formation in the Donetz basin, Russia, into seven zones by means of naiads and Conchostracans. The upper three zones contain characteristic Estherians and the fifth zone is designated by *Lioestheria* (?) *simoni*. Likewise JONGMANS and PRUVOST (1950) selected *Lioestheria* (?) *simoni*, *Euestheria cebennensis* plus *Leaia baentschiana* and *Asmussia tenella* as zone fossils respectively of Westphalian C, Stephanian A, and Autunian. (See also PRUVOST, 1925). GRAND'EURY's zonation of the Upper Carboniferous in Western Europe is shown in table VI. Thus there are several which are applicable more widely than merely local correlation.

In the Carboniferous *Kohlengürtel* of Eur-America, the Estherians are commonly associated with plants or naiads in the same formations, but it is not less common in other continents for them to occur without these associates. In the variegated or red formations extensive in the interior of the continents they are frequently found together with ostracodes and fishes. Correlation among these formations should rely upon the palaeontology of these assemblages. When a formation yields no other fossil but Estherians, their value as the key fossil is high.

I proposed a term *morphic index* (1944) for the morphic characteristic common among two or more species or genera, but their

Table VI. Zonation of the Coal Measures in Western Europe by means of Naiads and Conchostracans, (after GRAND'EURY)

Autunien	8. Zone à *Estheria tenella* et *E. hallyensis*
Stephanien	7. Zone à *Anthracomya stephaniensis* Assie de Rivede Gier 6. Zone à *Anthracomya calcifera* et *Leaia baentschiana*
Westphalien	Assie de La Houve 5. Zone à *Estheria cebenensis* Assie de Bruay 4. Zone à *Anthracomya phillipsi, A. wardi* et *Estheria simoni* (Dispersion des genres *Carbonicola* et *Naiadites*) Assie d'Anzin 3. Zone à *Naiadites carinata, Carbonicola similis, Anthracomya pulchura* et *Estheria dawsoni* Assie de Vicoigne { 2. Zone à *Anthracomya williamsoni* et *Leaia tricarinata minima*; 1. Zond à *Carbonicola acuta* et *C. robusta* } Assie d'Ardenne. Faune marine.

distribution is restricted to a certain geological age or province. For example, the distribution of eodiscids having tuberculated cephalic borders is confined to the Olenellian.

PRUVOST pointed out the mutation of *Leaia* with reference to the widening of angle α where the angles α and β (see fig. 29) are respectively defined as that made by the dorsal margin with the anterior and posterior carina (LASPEYRES, 1870). Angle α is 70° to 80° in the Dinantian, 90° in the Westphalian and 100° in the Stephanian. As warned by RAYMOND, the mutation of the genus in other regions, however, may be another story. A wide variation in the angle is seen among *Leaia* from a thin Permian bed in New South Wales.

These are a few examples of the morphic index for geological age or geographical province, but there are ecological ones. For instance, in the tropical forest nearly all of the broad leaves have entire margins, although compound or palmate ones are rarely found. Among woody plants the multilacunar nodal type occurs abundantly in the temperate zone and the unilacunar type in the tropical zone (SINNOT and BERRY, 1915). Such morphic characteristic regardless of taxonomy is a morphic index for ecology. Estherian faunas can also be an index of this kind. As will be discussed further in the next chapter, palaeo-

climatology is suggested by the carapace dimension, while the morphic diversity of an Estherian fauna which is indicated not only by the number of species or genera, but also by the angle of morphic diversity as defined later (page 77), shows an aspect of its environment. Therefore the number and the angle are two morphic indices.

CHAPTER III
Fossil Estherians in Eastern Asia

1. History of research and general statement

The first Estherian species described from Eastern Asia was "*Estheria*" *middendorfii* JONES (1863) from Transbaikalia. The collections from Eastern Siberia were successively studied by EICHWALD (1865), REIS (1909), and CHERNYSHEV (1930, '40).

Since YOKOYAMA's description of "*Estheria*" *rectangula* (1894) no Estherian had been found in Japan for a long time, until a few carapaces were discovered in the Mine series (KOBAYASHI and others, 1939). Recently Estherians were found at some places in the Inkstone series (IMAMURA and KUSUMI, 1951), but only a preliminary observation has so far been made on the material (HASE, 1948). Two species from the Atsu series however have been described (KOBAYASHI, 1952).

Estherians from Indochina and South China were described by MANSUY (1912, '21). Studies on Central and North Chinese and Mongolian ones by GRABAU (1923), COCKRELL (1924) and PRUVOST (1927) are compiled in CHI's paper (1931) which also dealt with fresh materials. In Korea 2 species have been described from the Daido group by OZAWA and WATANABE (1923).

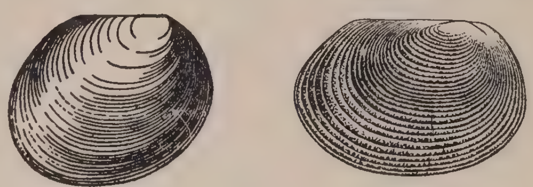
Since 1941 I have conducted a research project on the *non-marine Mesozoic formations in Eastern Asia and fossils contained therein* with SUZUKI, TAKAI and HANAI and carried out studies on Estherian collections with my students and assistants. The collections all from various localities in Korea and Manchuria were described in several papers by KOBAYASHI and HUZITA (1942), TANI (1943), KOBAYASHI and KIDO (1947), KOBAYASHI (1951) and KOBAYASHI and KUSUMI (1953). Simultaneously with these studies RAYMOND (1946) was making an extensive revision on the fossil Conchostraca and made some comments on the Siberian and Chinese species.

As discussed in the preceding chapter, RAYMOND appears to have split Estherians too far. Here I contend, however, that *Estheria* or *Estherites* s.l. should be classified into some genera, although such a classification is more artificial than natural at present, because distinction into form-genera is a step toward a better understanding of this difficult fossil group and consequently toward natural classification.

With this thought I restudied the species already described and new generic references are made in this paper. Estherians so far known in Eastern Asia comprise 48 species including 6 varieties and 4 formae which are distributed here among 9 genera and 3 families. Incidentally *Estheriella radiata* var. *multilineata* JONES, 1905, from Putus Semanggol near Taiping in Malaya is excluded from the Conchostraca, because it is an immature form of *Daonella moussoni* (KITTL) according to NEWTON (1925).

A Devonian Estherian seems to occur in the Wetwin shale in the Shan plateau of Burma (REED, 1929). The shale beds are intercalated in the thick plateau limestone and yield Middle Devonian marine fossils. The Estherian was found at Kyukmé with *Lingula* and plant remains and is said to be similar to *Euestheria mangaliensis*. This is the JONES's well known species (1862) occurring at Mangali and Mesa in the Wardha-Gondwana basin in peninsular India in a shale of the Damuda formation which is either late Permian (COTTER, 1938) or early Triassic (BROWN, 1938).

In North and Central China there are two Late Palaeozoic Estherians. One is *Euestheria mathieui* PRUVOST, 1927, from the upper Westphalian Tangshan formation in the Kaiping basin, Hopei, and the other is *Euestheria fukiensis* (GRABAU), 1924, from the Upper Permian Huk'ou shale in Fukien. All others are Mesozoic. *Euestheria middendorfii* from Tourga (or Turga) in Transbaikalia was first regarded to be a Tertiary (?) Estherian, but it is undoubtedly a member of the Jurassic Jehol fauna.



a b

Figure 15. Two Upper Palaeozoic Estherians in Eastern Asia.

a. *Euestheria mathieui* PRUVOST (after PRUVOST)

b. *Euestheria fukiensis* (GRABAU)

Recent studies on the non-marine Mesozoic formations and fossils in Korea and Manchuria enabled me to classify them into 5 groups by means of four distinct faunas and three distinct floras as shown in a table previously. (See page 163 of this journal, Vol. 8). Their ages were determined not only by various kinds of fossils, but also by the interfingering relation of non-marine sediments into marine ones. But it is still tentative and it is possible that the top division of a lower

Table VII. The limnic Mesozoic formations in Eastern Asia

Geological Age	Korea and Manchuria	Upper Amur, Mongolia, China and Indochina	
Palaeogene	Sungari	Tsagoiana	Iren Dabassu
Up. & Mid. Cret.	Kyöngsang	(Shevya)	Djadokhta
Low. Cret.		*intermedia-sinensis*	
Up. Jurassic	Jehol	Turga	Ondai Sair
Mid. Jurassic		Karabon	
Low. Jurassic	Daido	Kubekova	*zeili*
Up. Triassic		Trubachevo	*mansuyi*

group is contemporaneous with the basal part of an upper group.

I have tried to refer the Estherians from Transbaikalia, Indochina and other regions provisionally to one of these faunal groups. In these faunal groups there are two kinds. One consists of many species indigenous to each basin and the other of a smaller number of widely spread ones. What such a difference means is discussed at the end of this chapter.

2. The Daido Estherian fauna

Among the Mesozoic Estherians of Eastern Asia *Estheriina atsuensis* and *E. nakazawai* are the two oldest species which were found by NAKAZAWA in the Atsu series in Prov. Nagato (Yamaguchi Prefecture). Because the Estherian horizon is located below the *Halobia* shale containing *Halobia aotii*, the age of the horizon must be early Carnic, if not Ladino-Carnic.

Estheria zeili, *E. minuta* and its ally are reported to occur in South China and Indochina, beside an indeterminable one from the schistes à *Estheria* d'Anchau. When *E. zeili* (MANSUY, 1912), was found in the Estherian shale of Moug Hou Hai, Haut Laos, the shale was thought to be the Permo-Triassic passage bed, because of its resemblance with *E. mangaliensis*. Later, however, *zeili* was found between Yunnan-fu and Yuanyuangchin, Yunnan by SAURIN (1933) in a Triassic formation of 1,000 meters' thickness lying above the Permian formation. Therefore this Estherian bed is probably Rhaetic

and the thick red formation extends up possibly into Liassic (FROMAGET, 1934). Still later the *zeili* bearing red formation was found in Haut Laos to lie on the Carno-Noric with slight discordance between them (FROMAGET, 1941).

Estheria minuta by MANSUY, 1912, for which I proposed *Euestheria mansuyi* is found together with *Gervillia alloucheryi* and *G. haloensis* in limestone at Moncay in the Halo sheet area in Tonkin. The limestone was correlated with the Lettenkohle. In the P'ou Haut arc the marl containing this *E. minuta* merges with the nerito-paralic Noric beds (FROMAGET, 1941). *E.* cfr. *minuta* from a shale of Ban Hoc in the Soula sheet area, Western Tonkin (MANSUY, 1921) is, however, not well preserved. The illustrated right valve of this form is evidently expanded backward. If its outline is original, it is a long form more similar to *E. kawasakii* than to *E. mansuyi*. The indeterminable Estherian from the Anchau shale looks like *mansuyi* and is accompanied by *Gervilleia*, *Posidonomya*, *Pseudomonotis* (?) and others at Bin-Lieu. No taxonomic comment can be made on it because of its obscure illustration. There are two or more species in Indochina. *E. zeili* may be Rhaetic and *E. mansuyi* Noric.

Two other Triassic Estherians occur in Japan. DOI and OKUBO found a few ill-preserved ones at Kataobata near Hikiji, west of Asa, in Prov. Nagato. According to HASE (1951), the horizon of Kataobata containing *Euestheria kawasakii* and *Cyclestherioides koreanica* lies at the top of the middle Mine series. Because the upper Mine yields early Noric *Entomonotis scutiformis* (TELLER), the Estherian horizon must be either Upper Carnic or Carno-Noric.

Because the Daido series in Korea and its equivalent formations in Manchuria are all lacustrine sediments and because Liassic age is the conclusion which KAWASAKI arrived at on the basis of the Daido flora, the occurrence of these species in the upper Carnic stage is very important. *Euestheria kawasakii* and *Cyclestherioides koreanica* were originally described by OZAWA and WATANABE from the Tonjin formation of the Kimpo coal-field in Central Korea, a member of the Daido series of Korea. The Estherian shale is located in the Koyangi sandstone beds in the basal part of the Tonjin. Because the two species occur in Japan at the top of the middle Mine series, the age of the shale must be also late Carnic or Carno-Noric.

The Daido series in the Rampo area to the south of Kimpo consists of three cycles of sedimentation (KOBAYASHI, 1953). The Gabisan

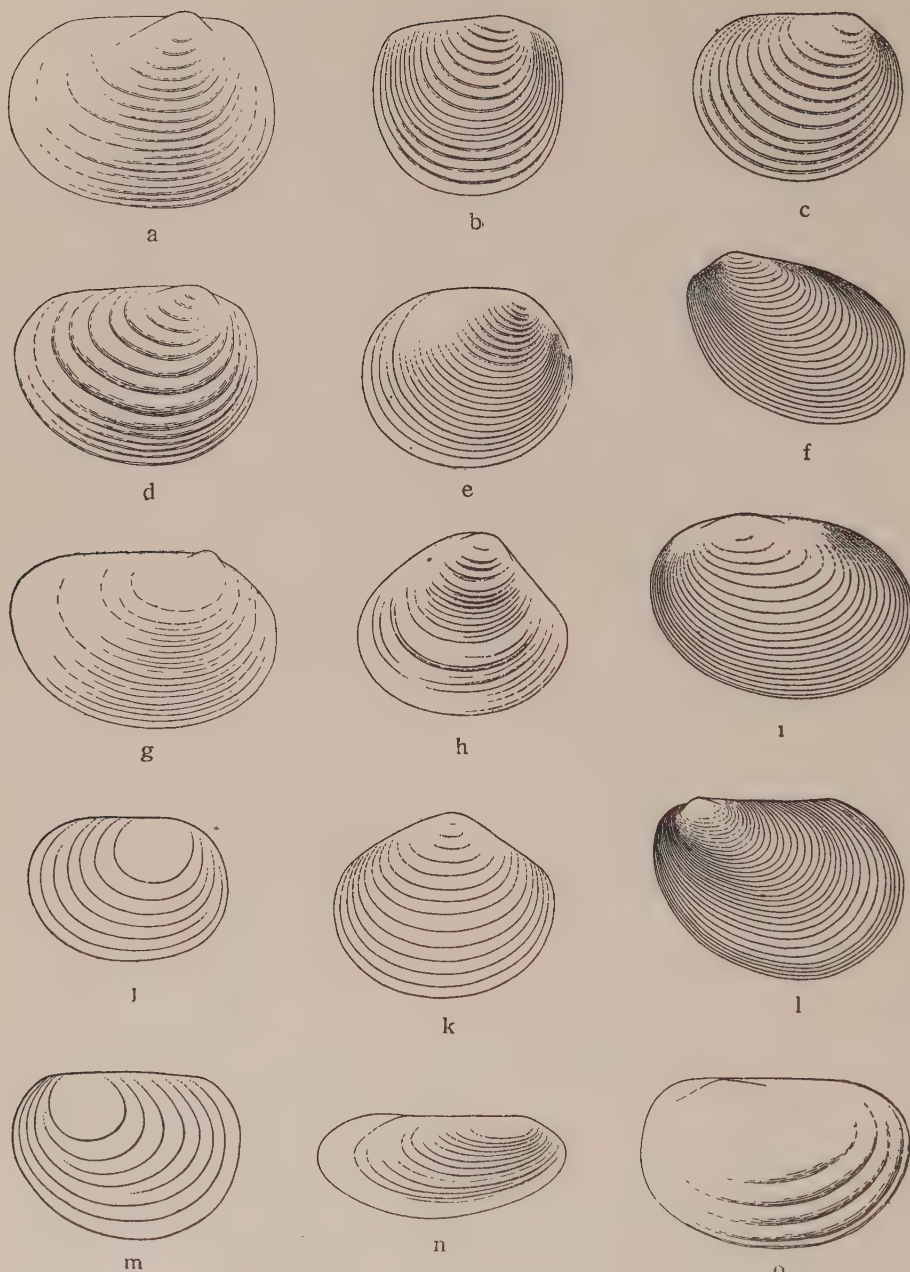


Figure 16. Estherians of the Daido group.

beds which represent the upper part of the lower cycle yields at Kinkoan *Cyclestherioides rampoensis* which is found also in the Koyangi beds in association with the two species above-mentioned. Therefore the Gabisan beds are approximate to the Koyangi beds in age, the conclusion being endorsed by the occurrence of such an archaeic type of plant as *Lobatannularia rampoensis* in the Hakuunsan beds located in the upper part of the middle cycle.

The occurrences of *Cyclestherioides* aff. *rampoensis* together with *Euestheria shimamurai* at Matienling, Laoyehmiao in Jehol and of the latter in the Chudo beds of the Daido series at Shindo in the Kenjiho area, North Korea, suggest that these Estherian horizons are likely to be upper Triassic.

The Kurori beds near Phöngan (Heijo) yield *Cyclestherioides cycloides* and *Euestheria tanii* beside *E.* aff. *reticulata* and *E.* aff. *transbaikalica.* Here the last two are distinguished as two new species, because the peculiar intercrossing of the concentrics in *E. reticulata* cannot be seen in *Euestheria kidoi,* n. sp. i.e. *E.* aff. *reticulata* by KOBAYASHI, 1951 and because *Euestheria kusumii,* n. sp. i.e. *E.* aff. *transbaikalica* KOBAYASHI, 1951, is taller than *E. transbaikalica* and has coarse radial striae in the interspaces. The Kurori beds belong to the Daido series, but whether the age of the beds is early Jurassic or late Triassic is difficult to say from these Estherians, as they are all new species. But the absence of late Triassic species might suggest the former.

The reference of *Asmussia khinganensis* from Heitingshan on the eastern slope of the central Great Khingan range to the Daido Estherian group is provisional. Similarly the indeterminable Estherians from Hsiahuayuan between Peking and Kalgan are brought into the Daido group, also quite provisionally, because they are incomparably smaller than any of the Jehol group in the same region.

Lioestheria krystofovichi from Southern Ussuri on the Andreev's

a. *Estherites heckeri* (CHERNYSHEV)
b. *Asmussia khinganensis* (KOBAYASHI)
c. *Euestheria kusumii* (KOBAYASHI)
d. *Euestheria zeili* (MANSUY)
e. *Cyclestherioides rampoensis* (KOBAYASHI)
f. *Euestheria tanii* (KOBAYASHI)
g. *Euestheria foveolata* (CHERNYSHEV)
h. *Cyclestherioides koreanica* (OZAWA and WATANABE)
i. *Euestheria shimamurai* (KOBAYASHI)
j. *Estheriina nakazawai* (KOBAYASHI)
k. *Cyclestherioides cycloides* (KOBAYASHI)
l. *Euestheria mansuyi* KOBAYASHI
m. *Estheriina atsuensis* (KOBAYASHI)
n. *Euestheria kawasakii* (OZAWA and WATANABE)
o. *Lioestheria krystofovichi* (CHERNYSHEV)

bay is a relatively large form, with punctate test, 8.5 mm. long at the largest. It may be a member of the Daido Estherians because the formation containing it is considered close to the below mentioned Estherian horizons of Khakharei and Kubekova.

In Transbaikalia there are at least four Estherian beds the lowest of which belongs certainly to the Daido group. *Estherites heckeri*

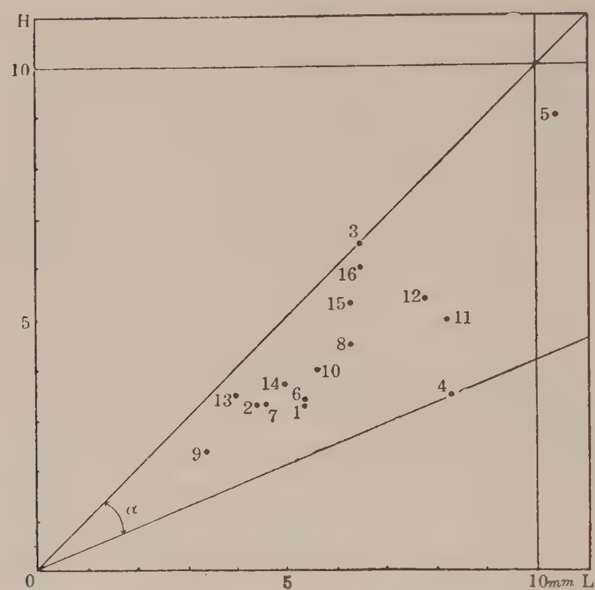


Figure 17. Height-length proportion of the Estherians in the Daido group. Angle $\alpha = 22°5'$

Estheriina atsuensis (KOBAYASHI)	Lower Carnic. (No. 1)
Estheriina nakazawai (KOBAYASHI)	ditto (No. 2)
Cyclestherioides koreanica (OZAWA and WATANABE)	Upper Carnic (No. 3)
Euestheria kawasakii (OZAWA and WATANABE)	ditto (No. 4)
Cyclestherioides rampoensis (KOBAYASHI)	ditto (No. 5)
Euestheria shimamurai (KOBAYASHI)	ditto ? (No. 6)
Euestheria mansuyi KOBAYASHI	Noric (No. 7)
Euestheria zeili (MANSUY)	Rhaetic (No. 8)
Estherites heckeri (CHERNYSHEV)	Rhaeto-Liassic (No. 9)
Euestheria foveolata (CHERNYSHEV)	ditto (No. 10)
Lioestheria krystofovichi (CHERNYSHEV)	ditto (No. 11)
Euestheria tani (KOBAYASHI)	Rhaeto-Liassic ? (No. 12)
Cyclestherioides cycloides (KOBAYASHI)	ditto (No. 13)
Euestheria kidoi KOBAYASHI	ditto ? (No. 14)
Euestheria kusumii KOBAYASHI	ditto ? (No. 15)
Asmussia khinganensis (KOBAYASHI)	Liassic ? (No. 16)

occurs in the lowest Estherian beds on the Gashimur river, at Trubachevo in Transbaikalia and also at Kubekova along the Yenissei. This and *Euestheria foveolata* from Khakharei, Tulunginsk district in gov. of Irkutsk are thought to be Rhaeto-Liassic. The former is a very small form with punctate interspaces while the latter is somewhat larger.

As listed here there are now 16 species in 6 genera in the Daido Estherian group, from Carnic to Liassic in age. They are distributed in an arcuate zone from the Yenissei tributary to Indochina through Irkutsk, Transbaikalia, the Great Khingan range, Southern Ussuri, the Korean peninsula and West Japan. As can be seen from comparison with the Jehol fauna, its morphic diversity is quite remarkable, as indicated not only by the number of genera and species but also in the inclusion of such aberrant genera as *Asmussia*, *Cyclestherioides* and *Estheriina*. The Yenissei-Transbaikalia, Koreo-Japan and Yunnan-Indochina are three major provinces which have their own indigenous species, none being common among them. Endemism is thus quite high in the Daido fauna. Still another characteristic of the fauna is the small size of these Estherians, if *Cyclestherioides rampoensis* which attains medium dimensions is excluded.

3. The Jehol Estherian fauna

Euestheria middendorfii is the leading member of this fauna. Because the age of the fauna has remained a moot question, I will start with a brief note on Mesozoic stratigraphy, although it has already been discussed in some detail elsewhere (KOBAYASHI, 1942). In Transbaikalia there are three facies in the post-Akiyoshi Mesozoic formations where one is marine. The two others are called the Algatchi facies and the tuffaceous or Estherian facies. The Algatchi facies is not pyroclastic and contains plant beds and coal seams. The formation of this facies is early Jurassic or even older because its florule is allied to the Daido-Mongugai flora. The Estherian facies is very pyroclastic. Its sequence consists of three parts, each beginning with a conglomeratic bed. The Karabon and Turga Estherian horizons are located respectively in the lower and the middle part. *Euestheria middendorfii*, *Ephemeropsis* and *Lycoptera* in the Turga horizon occur also in Mongolia, South Manchuria, North Korea, and North China in the Jehol group, always rich in volcanic material. The combination of the three fossils provides an important key to the correlation of

the Mesozoic non-marine formations in Eastern Asia.

The Kyöngsang formation in South Korea and West Japan, which is also rich in volcanic material, has been now proven to be mostly Lower and Middle Cretaceous. Its fauna is quite different from the Jehol fauna. In Shantung the Chinshan formation, a rough correlative of the Kyöngsang, overlies the Laiyang formation containing the Jehol fauna. Therefore the Jehol group must be older than the Kyöngsang, although Chinese geologists used to regard the Jehol fauna as early Cretaceous. The Jehol fauna, however, cannot be as old as Liassic, because in the Peipiao coal-field in Jehol, the Jehol group lies disconformably on the Peipiao coal-bearing formation which yields the Daido flora.

Thus the Turga horizon is either Upper or Middle Jurassic. Therefore the upper division of the tuffaceous facies in Transbaikalia, with the Selinda conglomerate at the base is possibly Lower Cretaceous. I cannot answer the question whether the Karabon horizon belongs to the Dogger or Lias, but its age is certainly not far from the boundary between the two epochs. The horizon yields *Euestheria transbaikalica* and *Euestheria reticulata* at Karabon pass below Pokrovskia. The former is only a little larger than *Lioestheria foveolata* and has radial lirae occasionally branching. The latter has a somewhat polygonal reticulation in the interspaces.

E. middendorfii first thought to be a Tertiary Estherian, must be middle or late Jurassic in age. It was established by JONES (1863) on the specimens from Turga near Nertschinsk, later found also on the Turga bank at the junction of the Igonda and Schilka, Patkham pass of the Pritaloki range, and so forth. EICHWALD's *E. orientalis* (1865) from the bank of the Turga, a branch of the Onon, which has an elliptical outline, smaller number of growth lines (ca. 18) and polygonal or punctate sculpture, was synonymized with *E. middendorfii* by REIS (1909), but it reveals forma *orientalis* (i.e. forma *subelongata*). Still later *E. dahurica* was found from the Turga horizon with *E. middendorfii* and *Lycoptera middendorfii* along the Uruliungui gorge (CHERNYSHEV, 1939).

As the Turga horizon belongs to the Jehol group, the paper shale of the Ondai Sair formation at Ussuk in Tsangan Nor region in Outer Mongolia which yields *Euestheria middendorfii* with *Lycoptera*, *Ephemeropsis* and other insects (COCKRELL, 1924) must be a member of the same group. COCKRELL's form belongs to forma *intermedia*.

E. middendorfii is reported by CHI (1931) from the Jasu Jergulung formation on Uliassutai trail on the border between Inner and Outer Mongolia, and from the Huanjen formation of Wutaohotze, in Liaoning, South Manchuria. His *Estheria middendorfii* var. *sinensis* from Pokenli, in North Manchuria, however, must be excluded from the Jehol fauna, because it is identified with *Estherites mitsuishii*, a member of the Sungari fauna (KOBAYASHI and HUZITA, 1942).

In Sinkiang there are three or more Estherian horizons. In the section of Fuyuanhsien the lower one lies in a Permian formation and two in a Lower Triassic formation. *Dicynodon sinkiangensis* and *Lystrosaurus murragi* were found in the middle one at Fuyuang (YUAN and YOUNG, 1937). It is overlain by conglomerate and sandstone beds, 38 m. thick. Above them come sandstone and clayslate beds, 280 m. thick, containing Estherians and then gray clayslate beds, 550 m., containing woods and fishes. Then there is another conglomerate 600 m. thick which is overlain by Rhaetic beds containing coal and plants (LEUCHS, 1937).

CHI (1931) described 2 Estherian species from the province. *Euestheria sinkiangensis* from a gray shale bed at Maiyaokou, northwest of Turfan, is accompanied by insect and plant remains. The other is *E. middendorfii* var. *sinensis* at Tikmadawn, northeast of Kuchar. Late Jurassic is suggested by him for the former which is a small form and early Cretaceous for the latter which is a little larger. True ages of these Estherians are, however, still uncertain. As Estherians are further known to occur in the Dzungarian basin and other places, they would be of great stratigraphical value in Central Asia, if a close study were made.

E. middendorfii has been a waste basket, and in fact it is a bad species very difficult to define, because it is so variable. With KUSUMI I studied a large collection procured from 15 localities in Barga, Jehol, South Manchuria and North Korea with the result that the following 3 varieties and 4 formae were distinguished beside the typical form:

Euestheria middendorfii (JONES)
" " var. *jeholensis* KOBAYASHI and KUSUMI
" " var. *elongata* KOBAYASHI and KUSUMI
" " var. *chii* KOBAYASHI and KUSUMI
" " forma *orientalis* EICHWALD
" " forma *peipiaoensis* KOBAYASHI and KUSUMI
" " forma *intermedia* KOBAYASHI and KUSUMI
" " forma *takechenensis* KOBAYASHI and KUSUMI

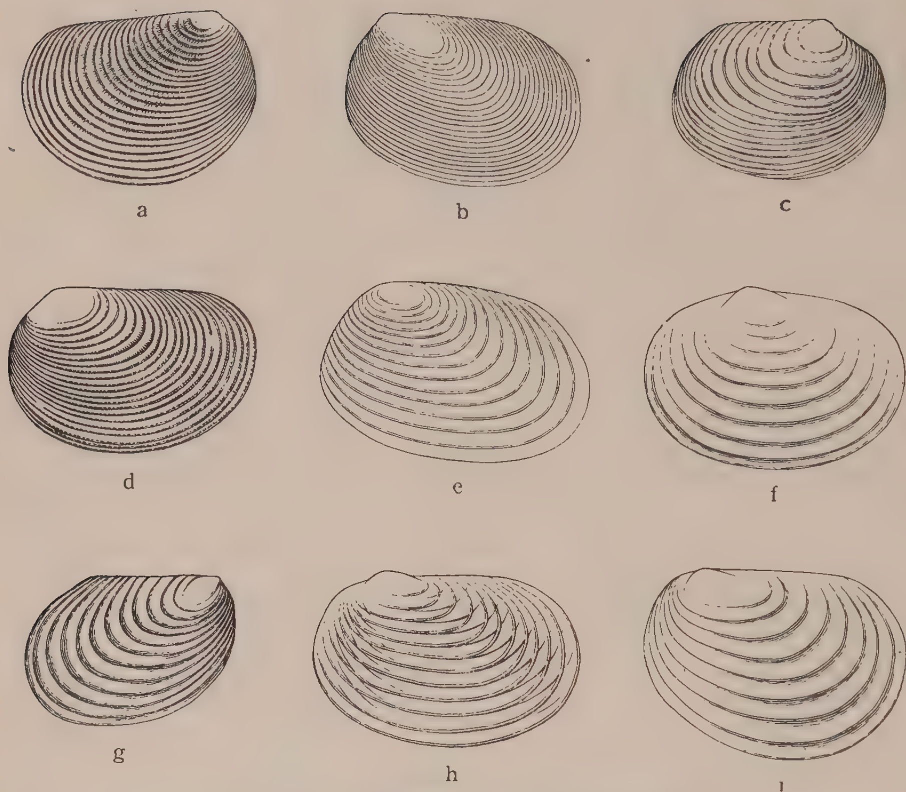


Figure 18. Estherians of the Jehol group. s.l.

a. *Euestheria middendorfii* (JONES) var. *sinensis* CHI
b. *Euestheria intermedia* (CHI)
c. *Euestheria kansuensis* (CHI)
d. *Euestheria middendorfii* (JONES)
e. *Euestheria middendorfii* (JONES) forma *orientalis* EICHWALD
f. *Estherites* (?) *dahurica* (CHERNYSHEV)
g. *Euestheria sinkiangensis* (CHI)
h. *Euestheria reticulata* (CHERNYSHEV)
i. *Euestheria transbaikalica* (CHERNYSHEV)

As discussed above, it is not a question whether the Kweichou formation is a member of the Jehol or the Kyöngsang group or whether the Karabon horizon belongs to the Jehol or the Daido group. The ages of the Estherians from Maiyaokou and Tikmadawn are also indefinite. Therefore the reference of the following species to the Jehol fauna is provisional:

Euestheria reticulata (CHERNYSHEV)
Euestheria transbaikalica (CHERNYSHEV)
Euestheria sinkiangensis (CHI)
Euestheria intermedia (CHI)
Euestheria middendorfii var. *sinensis* CHI (in part)

Euestheria middendorfii JONES var. *sinensis* CHI, 1931, is very widely distributed in North and Central China in association with *Estheria kansuensis* CHI, 1931, or *E. elliptica* var. *intermedia* CHI, 1931, at one or another locality. I think it proper to segregate *Euestheria intermedia* out of DUNKER's *Euestheria elliptica* as a distinct species as done by RAYMOND (1946). But a thorough study is needed to decide whether or not *sinensis* from Sinkiang, Hupei, Fukien and elsewhere is, as he thought, a species independent from *E. middendorfii*. At any rate it is noteworthy that *sinensis* is generally smaller than *E. middendorfii*. In Shantung it occurs in the Laiyang formation and in Kansu in the Liupanshan formation where *E. kansuensis* occurs. *Lycoptera* and *Asiatopsis* typical of the Jehol fauna, are their usual associates in North China.

E. middendorfii sinensis occurs further south in the Wuyi formation in Fukien, the Kweichow in Hupei, the Ts'ienfuyen in Szechuan and the Kienteh in the Chekiang where in the last two formations it is accompanied by *Euestheria intermedia*. Whether these formations in Central China which used to be collectively called the Kweichou formation, is Upper Jurassic or Lower Cretaceous is a question, because the naiads in the formations are allied to those of the Kyöngsang fauna. The Jehol fauna in the strict sense comprises, beside those listed on page 67, the following:

Estherites (?) *dakurica* (CHERNYSHEV)
Euestheria kansuensis (CHI)
Euestheria middendorfii var. *sinensis* CHI (in part)

In marked contrast with the Daido fauna the Jehol fauna s. str. consists of only 3 species in one or two genera. But *E. middendorfii* is an extraordinarily variable species comprising 4 varieties and 4 formae. They constitute a very distinct fauna with *Lycoptera* and *Asiatopsis*, which is distributed widely from Transbaikalia in the north, Kansu in the south, North Korea in the east and outer Mongolia or possibly Sinkiang in the west. If the Estherians from the Kweichou formation can be added to the fauna, the distribution is extended into Central China.

Another significant aspect is the large size of *E. middendorfii*. JONES' type measures 21.5 mm. in length and 13 mm. in height. The largest in my collection is 22.8 mm. in length and 14.3 mm. in height. In other words it is larger than the largest living Estherian, i.e. *Eoleptestheria ticinensis*, 20 mm. long and 13 mm. high.

Among the various forms of the species, the forms which grow

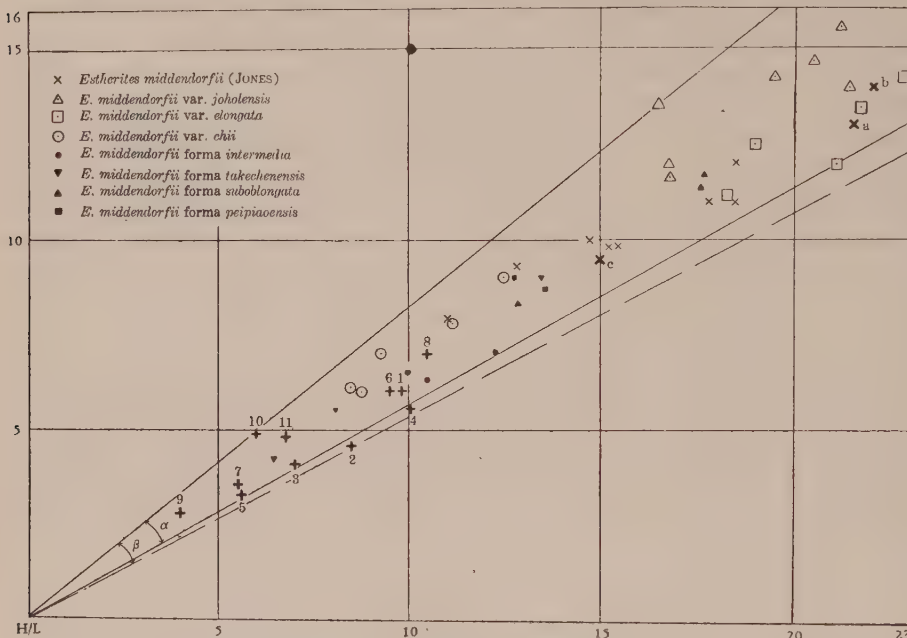


Figure 19. Height-length proportion of the Estherians in the Jehol group.

No. 1.	*Euestheria middendorfii* var. *sinensis*	from Sinkiang
No. 2.	ditto	from Shantung
No. 3.	ditto	from Kansu
No. 4.	ditto	from Chekiang
No. 5.	ditto	from Hupeh
No. 6.	ditto	from Fukien
No. 7.	*Euestheria intermedia*	from Sinkiang
No. 8.	ditto	from Chekiang
No. 9.	ditto	ditto
No. 10.	*Euestheria kansuensis*	from Kansu
No. 11.	*Euestheria sinkiangensis*	from Sinkiang
a.	*Euestheria middendorfii*	by JONES
b.	ditto	by REIS
c.	ditto	by CHI

$\alpha = 11° \ 5'$

$\beta = 13°$

larger than 15 mm. in length or 10 mm. in height are forma *typica*, var. *jeholensis*, var. *elongata* and forma *orientalis*. Their distribution extends from Transbaikalia to Jehol. Var. *sinensis* of the species, 9.6 mm. long, *Euestheria intermedia*, 10.5 mm. long and *Euestheria kansuensis*, 6 mm. long at the maximum are all smaller and their age is contemporaneous with that of the preceding ones or partly younger. They occur in North and Central China and Sinkiang. The Estherians from the Karabon horizon are older and still smaller. *Euestheria transbaikalica* is 7 mm. or less in length and *Estherites* (?) *reticulata* 5 mm. or less in height. *Euestheria singkiangensis* 6.8 mm. long and 4.8 mm. high is approximate to these two in size.

It is certainly interesting to see through the Jehol group s.l. that Estherian carapaces become larger in the Turga after the Karabon age. The maximum size is attained by the Estherians of the area from Transbaikalia to Jehol. Those further to the south or to the west are smaller, notwithstanding the fact that these Estherians are of about the same age.

4. The Kynögsang Estherian fauna

In Japan *Estheria rectangula* on which *Pseudoleaia* is instituted was first described by YOKOYAMA from Mizunuma, in the Yuasa basin, Prov. Kii (Wakayama Pref.) as early as 1894. Because none has since been procured from the basin or any other place in the outer zone of southwest Japan, it must be a rare drift in the paralic Ryoseki series of the Wealden age. No Jurassic Estherian has as yet been found in Japan. IMAMURA and KUSUMI, however, discovered Estherians at Inakura, northeast of Fukuyama in Province of Bitchu (Okayama Pref.) in the Yamaji shale in the upper part of the Cretaceous Inkstone series, which may be correlated to the upper Naktong or lower Shiragi series in South Korea. As I can judge HASE's preliminary study, there are at least three species as follows:

Estherites cfr. *naktongensis*
Euestheria cfr. *kyöngsangensis*
Cyclestherioides sp.

The Kyöngsang formation in South Korea can be divided into the lower or Naktong series and the upper or Shiragi series where the former is Lower Cretaceous and the latter Middle Cretaceous. Estherians are found in the Shikkoku-gun, Keisho-hokudo and at Kotanri,

Bunsan-men, Shinshu-gun, Keisho-nando and also in the Kasenri beds i.e. the lower part of the upper Shiragi series, at a railway cutting at Sanki near Akari, Seimen, Keisho-gun, Keisho-nando. In addition, Estherians are known to occur in Eido area in the Shiragi series. They are classified into 2 species and 3 varieties as follows:—

Series	Naktong	Shiragi
Euestheria kyöngsangensis	×	
Var. *huzitai*	×	
Var. *medialis*		×
Var. *paucilineata*		×
Estherites naktongensis	×	

E. naktongensis is a peculiar form more elliptical than *E. elliptica* and has a subcentral umbo. The outline is generally subovate and the umbo subterminal in *E. kyöngsangensis* and its varieties, but the outline is quite variable and accordingly the height-length proportion ranges from 1.29 to 1.62. Their growth lines are generally fine and as numerous as 40 except in var. *paucilineata* in which they number 20 to 25. The sculpture in the two species consists of radial lirae which are inosculating or branching.

In the Chientao area in the extreme southeastern part of Manchuria Estherians occur in two or more horizons in the Talatzu formation. In association with *Manchrichthys uwatokoi*, *Palaeolimnadiopsis kantoensis* was collected from its basal part at Latzukou, Sueifentien and Nanshan of Wangchinhsien. *Estherites endoi* from Talatzu seems to indicate a horizon in the middle Talatzu. Radial lirae or dots are found in the interspace of the latter species. The former species has also radial lirae, and the posterior outline is limnadiform. The dorsal margin is more or less concave behind the umbo.

The Talatzu basin is far from the Tsushima basin where the Naktong and Shiragi series were deposited. The Talatzu fauna is fairly distinct from either one of the latter two series, but *Trigonioides kodairaii*, a Naktong member discovered in the Talatzu series suggests early Cretaceous for the age of the Talatzu or its lower part.

The Estherian fauna procured at Kutsangkou near Fusung, in Tunghua region in South Manchuria comprises the following:

Euestheria aff. *kyöngsangensis* var. *paucilineata* (KOBAYASHI and KIDO)

Euestheria halobiformis (KOBAYASHI and KUSUMI)

Euestheria asanoi (KOBAYASHI and KUSUMI)

Euestheria nenkiangensis kutsangkouensis (KOBAYASHI and KUSUMI)

Euestheria (?) *lata* (KOBAYASHI and KUSUMI)

Cyclestherioides saitoi (KOBAYASHI and KUSUMI)

Cyclestherioides (?) *proamurensis* (KOBAYASHI and KUSUMI)

Asmussia tunghuensis (KOBAYASHI and KUSUMI)

As discussed already (KOBAYASHI and KUSUMI, 1953), they belong probably to the Kyöngsang fauna.

Euestheria daja (CHERNYSHEV)

Lynceus stchukini CHERNYSHEV

from Shevya in Transbaikalia are referred to the Kyöngsang fauna for the simple reason that they are said to be Lower Cretaceous species by CHERNYSHEV (1930).

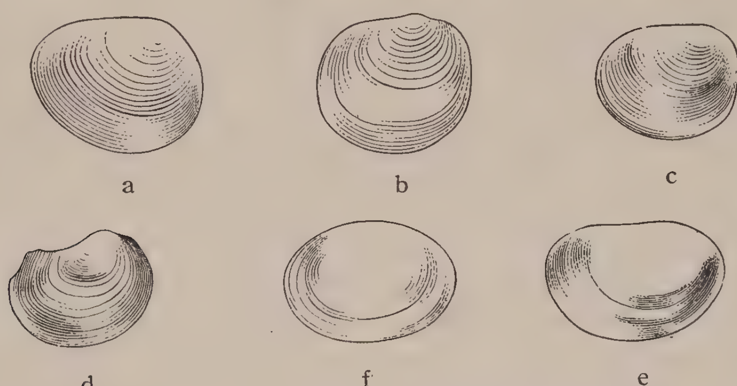


Figure 20. Estherians of the Kyöngsang group.

a. *Cyclestherioides* (?) *proamurensis* (KOBAYASHI and KUSUMI)
b. *Asmussia tuughuensis* (KOBAYASHI and KUSUMI)
c. *Cyclestherioides saitoi* (KOBAYASHI and KUSUMI)
d. *Palaeolimnadiopsis kantoensis* (KOBAYASHI and KIDO)
e. *Estherites endoi* (KOBAYASHI and KIDO)
f. *Estherites naktongensis* (KOBAYASHI and KIDO)

Thus the Kyöngsang fauna comprises 14 species and 3 varieties which are distributed in 7 genera, namely *Lynceus*, *Euestheria*, *Pseudoleaia*, *Asmussia*, *Estherites*, *Cyclestherioides* and *Palaeolimnadiopsis*. Not only in such morphic diversity, but also in the preponderance of indigenous species in each basin the Kyöngsang Estherian group is

similar to that of Daido, but in size the former is larger than the latter, because more than a half of the species and varieties attains a length exceeding 10 mm., though evidently smaller than the Jehol Estherians, because none of them reaches 13 mm. in length. Another significant morphic feature is the numerous growth lines, many of them having more than 20 and generally between 30 to 40 in *Euestheria kyöngsangensis*. Like the Daido fauna, the Jehol fauna occurs in basins aligned in a zone from Transbaikalia to West Japan through South Manchuria and Korea where in the south the Estherians occur in the paralic sediment as in the Yuasa basin in the outer zone of West Japan.

5. The Sungari Estherian fauna

The Sungari series is extensively distributed from the Central Manchurian basin to the Seja basin of the Upper Amur river through the North Manchurian plateau. Its age remained a moot question until a critical examination was made (KOBAYASHI and SUZUKI, 1942) and its fossils described (KOBAYASHI and HUZITA, 1942; SUZUKI, 1942; TAKAI, 1942). The major part of it is Cretaceous, instead of Tertiary, although the top of the formation might extend into the base of the Palaeogene. Formerly it was considered to be mostly Upper Cretaceous, but through HANAI's recent study *Cypridea* which is typical of Lower Cretaceous and Jurassic in Europe and North and South America, was found among the Sungari ostracodes. Therefore it is probable that the lower limit extends lower than used to be considered. The major part of the Sungari series, however, must be younger than the Kyöngsang series, because the two are different in fauna, facies and mode of deformation (KOBAYASHI, 1942). The series in the Seya basin yields several plant leaves suggesting alliance with the Laramie flora. Therefore it is presently my opinion that, if the Sungari series inclusive of the Tsagoiana in the Seja basin is located in a range from the Middle Cretaceous to the Palaeocene, this age-determination may not be too far wrong.

Incidentally Late Cretaceous *Manchurosaurus* which was first described from the marginal facies of the Tsagoiana series at Peiyai in the Seja basin occurs in Mongolia in the Iren dabasu formation. Accordingly it is probable that the Djadokhta between the Iren Dabasu and Ondai Sair formations may correspond roughly to the Kyöngsang

group in Korea and Manchuria.

The Tsagoiana formation on the Manchurian border on the opposite side of Kasatokina along the Amur river yields *Euestheria amurensis* and *Euestheria posidonomyoides*. RAYMOND split *E. amurensis* into the species proper, *Orthothemos ovalis* and *Limnadopsis sibericensis*. *O. ovalis* is referred here to *Estherites* and *L. sibericensis* to *Palaeolimnadiopsis*.

CHI (1931) described *Estheria nenkiangensis* and *Estheria middendorfii* var. *sinensis* from Pokenli, in Heilungkiang Prov., North Manchuria, where the latter belongs to *Estherites mitsuishii*. The former is referred here to *Euestheria*. In addition, *Estherites septentrionalis* and *Euestheria tatientzuensis* (TANI, 1943) are known from the Sungari series in Manchuria.

The outline is subquadrate in *E. mitsuishii* and *E. septentrionalis*, the latter having a high anterior. It is subovate in *E. nenkiangensis* and elliptical or oblong in *tatientzuensis*.

In *E. mitsuishii* and *E. septentrionalis* tubercles are more or less radially aligned in the interspace tending to be radial lirae.

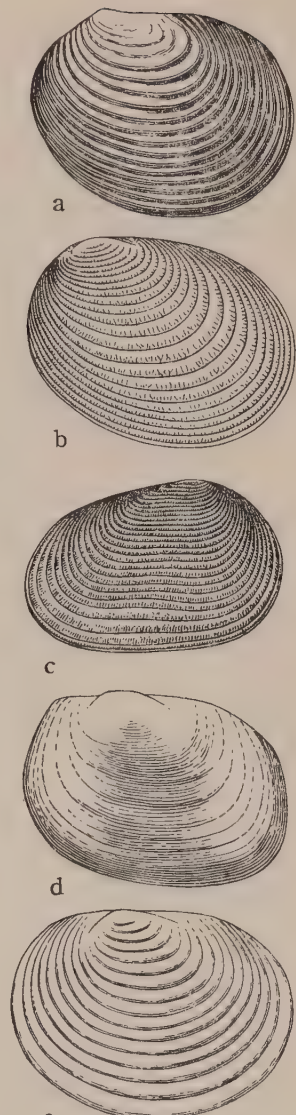


Figure 21. Estherians of the Sungari group.

a. *Euestheria nenkiangensis* (CHI)
b. *Euestheria septentrionalis* (KOBAYASHI and HUZITA)
c. *Estherites mitsuishii* (KOBAYASHI and HUZITA)
d. *Estherites posidonomyoides* (CHERNYSHEV)
e. *Euestheria amurensis* (CHERNYSHEV)

Those of *E. nenkiangensis* and *E. amurensis* are fine radial lirae which are branching. The irregular branching of *E. amurensis* similates the venation of plant leaves, while it is more regular in *E. nenkiangensis*.

In drill cores procured at Tiehli, near Peian, North Manchuria, it was found that *E. spetentrionalis*, *E.* aff. *nenkiangensis* and *E. mitsuishii* occur respectively at the depths of 55.3 m., 60 m. and about

66 m. from the land surface.

8 species in 3 genera of Estherians are so far known from the Sungari series. They are nearly all small forms less than 9 mm. long, although *Euestheria nenkiangensis* attains 11 mm. in length and 8 mm. in height. Four species from the Seya basin are smaller and about 5 mm. in length. Growth lines number less than 20 in most of them, though more than 20 in *Estherites septentrionalis* and 33 in the uncommon form of *Estherites mitsuishii*.

The specific list of the Sungari Estherian fauna is given below:

Euestheria amurensis (CHERNYSHEV)
Euestheria nenkiangensis (CHI)
Estherites posidonomyoides (CHERNYSHEV)
Euestheria tatientzuensis (TANI)
Estherites mitsuishii (KOBAYASHI and HUZITA)
Estherites septentrionalis (KOBAYASHI and HUZITA)
Estherites ovalis (RAYMOND)
Palaeolimnadiopsis sibericensis (RAYMOND)

Like the Estherians of the Daido fauna small forms are common in the Sungari fauna. Most of the Estherians from the Kyöngsang fauna grow a little larger and have more growth lines. If *Palaeolimnadiopsis sibericensis* is excluded, the remainder of the Sungri Estherians are quite monotonous. In this respect the fauna is thus quite different from the Daido and Kyöngsang faunas but similar to the Jehol fauna which the Sungari fauna resembles also in the mode of distribution. In other words Estherians occur extensively in the twin basin of Sungari and Seja, and are contained exclusively in limnic facies.

6. The relation between the orogenic cycle and the biocycle of Estherians

After the Akiyoshi orogeny in the middle Triassic period Eastern Asia became a center of distribution. As described in the preceeding pages, there are 46 species in the 9 genera of the Cyzicidae, Lioestheriidae and Limnadiidae. They constitute four groups of Estherian faunas as tabulated below. In looking over the Mesozoic Estherians in Eastern Asia, the facts can hardly be overlooked that the Daido Estherian fauna bears aspects similar to the Kyöngsang fauna while the Jehol and Sungari faunas resemble each other. In other words, the two different types of Estherian faunas appeared alternately twice. Therefore Estherian faunas can be combined in two suites as follows:

A. Shorin-Akiyoshi suite { A_1 Daido group
A_2 Jehol group

B. Taiho-Sakawa suite { S_1 Kyöngsang group
S_2 Sungari group

In both of the suites morphic diversity is great in the earlier groups where aberrant forms are common, whereas faunal aspect is monotonous in the later groups.

Morphic diversity is indicated by the number of species or genera in each Estherian group. In an attempt to figure out the degree of morphic diversity, I measured the angle between the lines passing through the points of maximum and minimum values of the length divided by the height. (See Table VIII). The angles of morphic diversity clearly show the alternation of the two kinds of faunas.

Table VIII. Mesozoic Estherian faunas in Eastern Asia.

Estherians / Faunal group	No. of genera	No. of species	No. of varieties	No. of formae	*Euestheria*	*Lioestheria*	*Asmussia*	*Estherites*	*Cyclestherioides*	*Estheriina*	*Palaeolimnadiopsis*	*Pseudoleaia*	*Lynceus*	Angle of morphic diversity
Daido	6	16			6	2	2	1	3	2				22° 5′
Jehol	2	8	3	4	7+7			(1)						11° 5′
Kyöngsang	7	13	3		5+3		1	2	2		1	1	1	16° 5′
Sungari	3	8			4			3			1			13° 5′
Total	9	46	6	4	20+10	2	3	(7)	5	2	2	1	1	

As shown in figure 22 the earlier group is distributed in isolate basins aligned in a zone along the margin of the continent at the time. Therefore Estherians occur not only in limnic but also in paralic facies along the Pacific basin. The distribution of the later group on the other hand is not so discontinuous, but extensive in a large depression in the interior of the continent. All Estherians are thus contained in lacustrine sediments.

Although the tectonics of Eastern Asia is not a subject for discussion in the present thesis, a brief mention is necessary here if we are to comprehend the relation between the biological and orogenic cycles. As described in great detail in my "*Sakawa cycle*", 1941, the Japanese islands present a typical example of *the migration of the*

Figure 22. The distribution of the Mesozoic Estherians in Eastern Asia and its relation to palaeogeography.

geosyncline. The primary Chichibu geosyncline developed into the Akiyoshi mountains through an orogenic cycle of the same name, while at the same time the geosyncline migrated to the front or to the oceanic side of the mountains. The secondary Shimanto geosyncline thus introduced became the Sakawa mountains in the Sakawa cycle and the geosyncline migrated again to the oceanic side. Subsequently the Yeso geosyncline in North Japan and the Nakamura geosyncline in West Japan developed into folded mountains.

The structure of these mountains is similar to one another in respect of their being an uniaxial anticlinorium with a metamorphosed axis in each. The processes by which these mountains were formed are also similar to one another. Each of these orogenic cycles consists of three major phases, namely *prorogeny* or geosynclinal subsidence, *euorogeny* or paroxysm of the cycle, and *metaorogeny* or instability in the settling of the newly built mountains. *Synorogeny* here designates a crustal movement in the already existing mountains, which is sympathetic with euorogeny in a later geosyncline and *interorogeny* means a movement which takes place in the mountains before and after synorogeny.

The history of development in the *Koreo-Chinese heterogen* is somewhat different and more complicated, because it is a heterogeneous aggregate. As illustrated in the history of Korea (KOBAYASHI, 1953), the Heinan and Yokusen geosynclines were folded by the Shorin and Taiho disturbances which correspond respectively to the euorogeny of the Akiyoshi and Sakawa cycles, but their modes of deformation

were quite different from those of the geosynclines in Japan. The Heihoku, Keiki and Reinan massives were not so strongly deformed and their modes of deformation are quite different. As I expect to discuss these types of deformations at some future date, I wish here to distinguish simply the epochs of the disturbances and the undulations or *Grossfaltung* in their intervals, and to show their time relation to the orogenic cycles in table IX.

Table IX. The relation between the biological and orogenic cycles in the Mesozoic history of Eastern Asia.

Geological age	Estherian		Koreo-Chinese Heterogen	Orogenic zones of Japan		
	Suite	Group		Akiyoshi	Sakawa	Oyashima
Neogene			Disturbance	Synorogeny II	Synorogeny I	Euorogeny
Palaeogene			Undulation	Inter-orogeny II	Interorogeny I	
Upper Cret.	Sakawa-Taiho	Sungari			Metaorogeny	Prorogeny
Middle Cret.						
Lower Cret.		Kyöng-sang	Taiho Disturbance	Synorogeny I	Euorogeny	Sakawa cycle
Upper Jura.	Akiyoshi-Shorin	Jehol	Undulation	Inter-orogeny I	Prorogeny	
Middle Jura.						
Lower Jura.						
Upper Trias.		Daido		Metaorogeny	Akiyoshi cycle	
Middle Trias.			Shorin Dist.	Euorogeny		
Lower Trias.			Undulation	Prorogeny		
Permian						
				Chichibu	Shimanto	Nakamura
				Geosyncline		

The biocycle of the Mesozoic Estherians in Eastern Asia indicated by alternation in morphic diversity parallelled the orogenic cycle. There is some time-displacement between the two cycles, because the orogenic fauna is more related to orogeny in the peri-continental zone and so is the inter-orogenic fauna to interorogeny in the intra-continental terrain.

As suggested by their names, the earlier groups of the Shorin-Akiyoshi and the Taiho-Sakawa suites correspond to the epochs of

crustal mobility in Eastern Asia. More precisely, the Kyöngsang group is contemporaneous with the grand Sakawa euorogeny and the age of the Daido group corresponds to the latter part of the Akiyoshi cycle as well as to the ensuing period when the crust was still labile. The Jehol period is the interval between the two orogenies and the Sungari period belongs to the latter part of the Sakawa cycle. Therefore it can be said that *the eariler groups are synorogenic faunas in the pericontinental zones whereas the later groups are interorogenic faunas in the intracontinental depressions.*

Through the Akiyoshi cycle of orogeny the Mongolian geosyncline became land, leaving the Amur geosyncline where a new sequence starts with the Upper Triassic marine formation (KOBAYASHI, 1942). In South Manchuria and Korea the deformation of the Middle Triassic Shorin phase was especially strong in the Heinan-Liaotung geosyncline (KOBAYASHI, 1951). In the Chichibu geosyncline paroxysm came in the Ladinic epoch in Japan (KOBAYASHI, 1941), but in the Noric or Carno-Noric in Indochina (FROMAGET, 1941; KOBAYASHI, 1952). The Upper Triassic and Lower Jurassic formations containing the Daido group of Estherians are sediments in separate basins within the mountains introduced by the Akiyoshi orogeny. Isolation of the habitats and differences of environments must thus be the principal reason why many indigenous species including aberrant forms were introduced. Some carapace drifts were imbedded in paralic sediments in the embayments.

All of the Jehol Estherians occur in limnic facies of sediments because their habitats were in a large inland depression probably embraced by the mountains uplifted by the *Grossfaltung* at the end of the orogenic cycle. Estherians are contained in lacustrine sediments in several basins within the large depression interior to the axis of uplift but the basins were presumably intervened by transmigratory mountain ranges in view of the great polymorphism of *Euestheria middendorfii.*

The Kyöngsang formation was accumulated in the hinter basin of the Sakawa mountains. The Talatzu series as well as the unnamed formation of Kutsangkou are lacustrine deposits in the intermontane basins. The environment of Shevya in Transbaikalia may not have been very different from them. These basins are so widely apart from one another that they produced their own faunas through isolation and endemism.

The Sungari Estherian group thrived in the Seya-Sungari twin basins which was, as discussed elsewhere (KOBAYASHI, 1942), introduced after the Amur embayment became land. This fauna like the Jehol fauna, is of the interorogenic type in its aspects, that is, morphic diversity is low and the number of species and genera is small, if compared with the synorogenic faunas of Daido and Kyöngsang.

In 1942 I discussed the Mesozoic climate in Eastern Asia with reference to flora. As a continuation I have shown the rise and fall of plants from the late Palaeozoic to the Triassic period and elucidated the floral evolution by climatic and palaeogeographic changes (1951). The Daido group is the most important coal-bearing one of the Mesozoic formations in Eastern Asia. The Daido group of floras in the paralic zone of Eastern Asia indicates a monsoon climate. The gradual decrease in the number of species of the Dipteridaceae relative to the total of flora indicates that the climate became tropical in Tonkin and subtropical in West Japan in the late Triassic period. It became colder further north then, as it probably did also in the early Jurassic. It was more arid in the interior of the continent. Climate in the epicontinental zone in the Daido epoch was presumably too humid, and in the south too warm, for Estherian life, these unfavourable conditions probably causing dwarfing. The larger part of the Estherians I examined are contained in black or carbonaceous shales, probably deposited in swampy grounds.

Insofar as I can judge from the Toyora floral group (KOBAYASHI, 1938) or the *Onychiopsis* suite (OISHI, 1939), the climate in Japan from middle Jurassic to early Cretaceous may have become generally a little cooler than before, although it was very warm along the Pacific coast where the great barrier reef existed in the late Jurassic and Wealden period.

The climate in the inland depression at the time is, however, difficult to determine from fossil plants, because aridity depauparates plant remains toward the interior of the continent. The gigantic Jehol Estherians do, however, suggest a certain kind of climate. Because the hypertrophy of Estherians is met with at present in inland basins in warm temperate zones, the basins in Transbaikalia, Barga and Jehol must have enjoyed a similar climate. The Estherians of the Jehol group are contained in variegated rocks. Carapace, however, becomes smaller in the Kweichou formation in central China, probably because it was warmer.

The Yuasa basin whence the peculiar *Pseudoleaia rectangula* was procured, belonged evidently to a tropical or subtropical monsoon region, because at Fujinami just behind the Estherian locality there was a luxuriant forest and no year ring is found in coniferous plants.

The Kyöngsang formation is a sediment in the hinter basin of the Sakawa mountains. Its lower division is the Naktong series which yields plants belonging to the *Onychiopsis* suite and year rings are seen in *Xenoxylon*. The climate suggested by them is warm and temperate. At the transition from late Jurassic to early Cretaceous when coal measures were accumulated in the Fushin and other coal fields it must have been more humid than before or after, even on the continent. It became probably more arid in the Shiragi epoch in which the red rocks are predominant. The Estherians from the Kyöngsang group and its equivalents in Korea and South Manchuria are not as large as those of the Jehol group, but as they are the second largest, the climate of their habitats must have been favourable, although worse than the optimum in the Jehol epoch.

As discussed elsewhere (KOBAYASHI, 1942), the Sungari series is a sediment in a large inland depression which was brought into being after the Sakawa orogeny. The Estherians therein are mostly smaller than those of the Kyöngsang group, but this does not mean simply the lowering of the temperature in hot season in the whole of Eastern Asia, because cycads are found in Japan and the Sungari-Seya basin is located far to the north. The climate of the basin may have been arid and less warm than that of the Tsushima basin in the Kyöngsang epoch. The mean size of Estherians is smaller in the Seya basin in the north than in the Sungari basin in the south. Estherians are widely distributed in the twin basins of Sungari-Seya and have generally less number of growth lines than those of the Kyöngsang group. As suggested already, the Estherians of the Sungari group may have been eurypic as compared with those of the Kyöngsang group.

In conclusion it may be said that morphic diversity of Estherian fauna is intimately related to isolation and endemism due to habitat localization caused by orogeny. *The size of the carapace* on the contrary *is a morphic index to palaeoclimatology.*

Of course there may be several factors for hypertrophy, but it is highly probable that the climatic factor is, insofar as can be judged from geological and palaeontological records, the leading factor

for that of the Estherian carapace, as indicated by the size, mean or maximum, of the carapace in the Jehol Estherian fauna. The climatic change in the continental interior which brought about the hypertrophy of Estherians is, however, also related to the change in land form caused by crustal movement, because the large, arid, inland depression in which the large Estherians flourished was produced by the *Grossfaltung* which in turn is related to the batholithic invasion of granite after the orogenic paroxysm.

CHAPTER IV
Distribution of the Non-Marine Conchostraca

1. General aspect of the distribution

As summarized above, only 2 or 3 species of Estherians are known from the Upper Palaeozoic in Eastern Asia, but if the Conchostraca are considered as a whole, they are Neo-Palaeozoic animals. Not only Estherians but Leaians have also developed greatly since the Devonian period. Their distribution is intimately related to the Old Red Sandstone in the Devonian and the Coal Measures in the Carboniferous period. In fact all of the Devonian Conchostracans are distributed along the *Old Red Gürtel* of Eur-America so-called by KOSSMAT (1936), if an undescribed one from Burma is excluded. Likewise most of the Carboniferous ones are distributed along the *Kohlengürtel* of Eur-America which extends from the Ural mountains to the middle continent of North America, and includes the Atlas in North Africa, although one is known in North China and a few from Mozambique and Zambezi are considered Stephanian, if not Permian. The number of Conchostracan species attained its maximum in the Pennsylvanian or Upper Carboniferous in the northern continents.

In the Permo-Triassic period the creature was distributed most widely in the northern and southern continents. It is known from Central China, Chatanga-Anabar, Tungusska and Kuznetsk basins in Central Siberia, Russia, Dyas or Trias basin behind the Variscan or Vinderian mountains in Europe, in the Atlas in North Africa, Newark basins in the axial zone of the Appalachians and Oklahoma and Kansas to the north of the Arbuckle-Ouachita mountains. In the Gondwana land the Conchostracans are known from the continental basins of peninsular India, Madagascar, Congo, Angola, and others of Africa and Brazil, and further, in the Andes and eastern Australia which belong to the circum-Pacific *Faltengürtel*. In the Permian period the Conchostraca developed more in the later part than in the earlier. The Leaiadidae died out at the end of the Permian period, leaving a relic in the Buntsandstein. Estherians thrived in certain regions in the early Triassic and in some others in the late Triassic period. The distribution of Estheriellians is very discontinuous, apparently representing independent branches from the Estherian stock.

After the Rhaeto-Liassic epoch, Estherians declined in most parts

of the world. The Bahian or Neocomian of Brazil yields 4 species; only 3 species are known from Africa and 1 species from India. As far as I am aware, these eight species are all that have been so far described from the Jurasso-Cretaceous of the southern continents. In Europe there are five Jurasso-Cretaceous species, namely,

(1) *Estherites concentrica* (BEAN) from the Jurassic of Yorkshire in England.

(2) *Euestheria murchisoniae* (JONES) from the Oxfordian of Scotland.

(3) *Lioestheria andrewsi* (JONES) from the Wealden or Purbeckian of England.

(4) *Euestheria subquadrata* (SOWERBY) from the Purbeckian and Wealden of England.

(5) *Euestheria elliptica* (DUNKER) from the Neocomian of Hannover in Germany.

In the holotype (fig. 1) of JONES' *andrewsi* the beak is evidently located below the dorsal margin as in *Cornia*. The test is punctate. JONES' *elliptica* in fig. 3 on pl. 4, in his monograph is much taller than the others in the same plate and possibly a distinct species of *Cyclestherioides*.

Estherians were obtained from the cores of borings from different horizons in Louisiana in which IMLEY (1941) recognized three forms resembling SOWERBY'S *E. subquadrata*, JONES' *E. murchisoniae* and *E. forbesii*, but none received new names. Little is said about the sculpture and the description does not permit any comment. Thus some 15 species constitute the total of Estherians outside of Eastern Asia where 48 species in addition to 10 varieties or formae are known. This is certainly a remarkable contrast.

This chapter summarizes the Conchostracan faunas according to age and area and attempts to figure out the faunal aspect. Special attention is paid to morphic diversity and variation in size and growth lines, because they are suggestive of climatic and palaeogeographic changes. The diversity is indicated by the number of species and genera. Thus this review necessitates a taxonomic revision which is especially difficult in the case of Conchostraca because, without the specimens, description and illustration alone are not always adequate.

There is, however, a considerable difference in the identification. *Estheria ovata* is an example. It is one species for a lumper but 5 species for a splitter. Therefore a statistical study cannot be undertaken without any comment, but I fear some comments given here

may be superficial. A series of papers by JONES and RAYMOND's compilation were especially helpful in carrying out this study.

As shown in the Estherian faunas of Eastern Asia, numerous genera and species do not always mean prosperity, because Jehol Estherians are large but belong to a few species while there are many small forms in the Daido fauna. RAYMOND did an interesting calculation. As he found 113 carapaces of *Lioestheria raaschi* on a slab of 9 square inches, it meant 50,263 to 155,400 individuals to a square mile. Such calculation, however, may not yield true population, because, as discussed already, a biocoenosis and thanatocoenosis can be totally different, especially in the case of Estherian banks. Frequency of occurrence is not given in many description, nor very helpful in such a survey of Conchostracans even if given.

More important are morphic diversity and variation of size, but it is dangerous to jump to any conclusion in palaeoclimatology or palaeoecology simply from these facts. All of the other available facts on stratigraphy and tectonics should be brought into consideration. My knowledge of the geology of the regions dealt with in this chapter is limited, but I have tried to add as many necessary supplementary statements as possible.

It is noteworthy that there are two kinds of fauna. One is the fauna of the orogenic zone and the other the fauna of the kratonic tarrain. The latter is similar to the afore-mentioned interorogenic fauna but there can be no doubt polymorphism will be more typically seen if a further study is made. The latter belongs to orogenic fauna when observed roughly but a closer observation will enable one to analyse it into orogenic and interorogenic faunas.

2. Conchostracans in the Old Red *Gürtel* of Eur-America

If *Rhabdostichus buchoti* which PÉNEAU (1937) thought to be Gotlandian *Estheria* is ignored, there is no Estherian in the Gotlandian. If an undescribed Estherian (REED, 1929) from the Wetwin shale in the Shan States of Burma is excluded, all of the Devonian Estherians occur on the Atlantic side in limno-paralic zones.

Euestheria stockmansi is described from the Lower Devonian of the Ardennes, containing *Spirobis*. (MAILLIEUX, 1939). *Lioestheria diensti* GROSS (1934) from the early Middle Devonian of Eifel (lower Eifelian Klerfer Schichten) was first listed as *Paracyclas rugosa* GOLD-

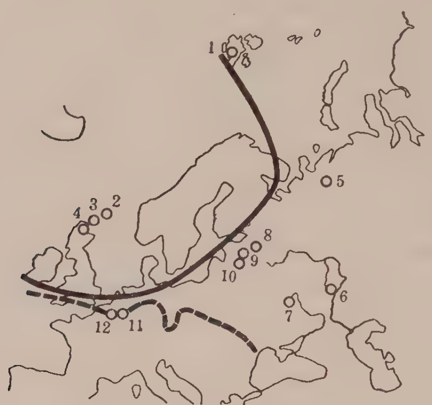
FUSS by MAUZ (1933) and later split into 3 species by RAYMOND (1946). His *Pseudestheria subcircularis* is founded on the specimen in fig. 6 which is, however, said by GROSS to be secondarily compressed. The present outline is subcircular and the umbo subcentral, instead of terminal as in *diensti*. It appears more likely that it is a *Cyclestherioides* rather than an *Asmussia*. Because *Cyclestherioides subcircularis* (RAYMOND) is a homonym of CHERNYSHEV's, *Cyclestherioides grossi* is proposed for the former. In the specimen in fig. 2 for which RAYMOND proposed a new name, *Palaeolimnadiopsis* (?) *eifelensis*, the outer growth lines swing back, very probably due to secondary deformation or squeezing. Because the outline of the carapace indicated by the inner lines is not much different from that of *diensti*, it is doubtful whether *eifelensis* is a distinct species.

Asmussia membranacea was described by PACHT (1849) from the Middle Devonian sandstone of Livonia, lying disconformably on the Gotlandian. Since then its wide distribution in northern Scotland, the Orkney and Shetland islands and the northern Catskill mountains of New York has been reported, but the Middle Devonian one from the Caithness flags in Scotland and adjacent islands were later distinguished as *Asmussia murchisoniana* (JONES, 1859) and the Middle Devonian one of the Catskills was recently segregated from the species as *Asmussia clarkei* by RAYMOND.

Radial ribs appeared in the Conchostraca already by the Middle Devonian. Two species of *Praeleaia* (*quadricarinata* and *quinquecarinata*) are found in Esthonia and Leningrad regions (Narova, Snetnaya, and Luga beds) in addition to LUTKEVICH's *Asmussia pogrebovi*, *Asmussia sinuata*, *Asmussia* (?) *vulgaris*, *Euestheria plicata* and *Euestheria crassa*. In the Upper Devonian (Stchigry and Petino beds) Estherians are widely spread out from Timan to the Lower Volga and the Don, as indicated by *Estheria rotundula*, *E. vulgaris*, *E. petinensis*, *E. elegantula*, *E. timanica* and *E. excentrica* (LUTKEVICH, 1937, '41) where *rotundula*, and possibly *timorica*, *excentrica* and *vulgaris* are *Asmussias* and *petinensis* and *elegantula* may be *Lioestherias*. RAYMOND is of opinion that *Asmussia sinuata* is a pathologic form of *A. porgrebovi*.

The Devonian Conchostracan list may be complete, if *Asmussia nathorsti* (JONES, 1883) from dark-coloured micaceous and carbonaceous shale in the Middle Devonian Old Red Sandstone at Mimers dal, Eisfjord region in Spitzbergen, is added to them. Because *Leperditia* is

found in the immediately subjacent formation (FREBOLD, 1935), it may have lived not far from the seashore.



1. Spitzbergen (Eisfjord)
2. Shetland islands
3. Orkney islands
4. North Scotland
5. Timan
6. Lower Volga
7. Don
8. Leningrad region
9. Esthonia
10. Livonia
11. Eifel
12. Ardenne

Figure 23. The Devonian Conchostracans in the Old Red *Gürtel* of Europe.
Thick line: Northwestern limit of the Devonian marine transgression on the continent.
Broken line: Southern limit of the distribution of the Old Red Sandstone.

In summarizing, it can be said that there are at least 18 species of Estherians and 2 of Estheriellians. A half or more of the Estherians belong to *Asmussia*, but the genus is not restricted to the Devonian as considered by RAYMOND. Most, if not all, Devonian Estherians are distributed along the so-called Old Red *Gürtel* which was an outcome of the Caledonio-Acadian orogenies. One from Burma is an exception, but it is probable that clastic Wetwin shale was wedged into the great plateau limestone by the Kwansi disturbance in Southeastern Asia (TING, 1929, KOBAYASHI, 1952).

LUTKEVICH (1937) contends that Conchostracans lived in the brackish water of the eastern Baltic which, however, is difficult to prove. On the other hand it is certain that at least a part of them lived in fresh water, because they occur in Scotland and adjacent islands which were located beyond the strand line at the Devonian marine transgression.

3. Conchostracans in the *Kohlengürtel* in Eur-America

It is indeed a remarkable event in the earth history that the coal measures were accumulated in the limnic and paralic zones of the Variscan mountains in the Carboniferous period. Conchostracans flour-

ished greatly in these coal basins. Their occurrences are known in the Donetz basin in Russia, in the Iberian peninsula and in the Atlas mountains in North Africa. In the Mississippian, the postorogenic basin in Nova Scotia which was produced after the Acadian disturbance yields Conchostracans. In North America, the number of Conchostracan species attained its maximum in the Pennsylvanian, if the Newark ones are reduced by synonymy as was done by BOCK, (see page 95). The great development of Conchostraca in the trans-Atlantic *Kohlengürtel* which extends from the middle continent of North America to Kamensk, east of the Urals, has no counterpart either before or after the Carboniferous.

RAYMOND's extensive revision of the Conchostraca in the *Gürtel* is the basis of this part of the chapter, as I do not have much personal opinion on the subject, but some comments are added as they arise in my mind. Furthermore information is given as to several species which he has overlooked. Because his revision of the European forms was apparently made on the basis of literature on the subject, some of the species which he has split may be combined when a study is made on the types or fresh material.

a. North America

Carboniferous Conchostracans of North America were greatly amplified by RAYMOND. There were only four described by LEA (1855), MEEK and WORTHEN (1868), JONES (1870) and CLARKE (1900), but now there are 10 Pennsylvanian species and 6 Mississippian species, the latter listed below all having been procured in the Cheverie formation of Nova Scotia.

Euestheria dawsoni (JONES)
Asmussia alta (RAYMOND)
Asmussia (?) *belli* (RAYMOND)
Eoleaia leaiformis (RAYMOND)
Eoleaia laevicostata (RAYMOND)
Leaia sp. indet.

As noted by RAYMOND two radial ribs are weak in *laevicostata* and still more so in *leaiformis*, suggesting the derivation of incipient radial carinae on a broad Estherian.

Pennsylvanian Conchostracans

Cyclestherioides blackstonensis RAYMOND, Rhode Island

Cornia ortoni (CLARKE), Ohio
Leaia haynesi (RAYMOND), Rhode Island
Leaia normalis (RAYMOND), Rhode Island
Leaia leidyi (LEA), Pennsylvania
Leaia asleyi (RAYMOND), Pennsylvania
Leaia leavis (RAYMOND), Pennsylvania
Leaia tricarinata MEEK and WORTHEN, Illinois and Indiana
Leaia wellerorum (RAYMOND), Illinois
Leaia acutangularis (RAYMOND), Rhode Island
Monoleiolophus conemaughensis, KOBAYASHI, nov. Pennsylvania

As listed above, there are more Leaians than Estherians in the Pennsylvanian and more than a half of the Leaians have arcuate ventral margins, which is why RAYMOND referred them to *Hemicycloleaia*. *Monoleiolophus conemaughensis* is a new name proposed for *M. unicostatus* RAYMOND, 1946, because of its homonymy with *M. unicostatus* (REED), 1927.

Finally, *Leaia silurica* MATTHEW (1910) from the lower *Cordites* shale in the Little River group of New Brunswick is a tricarinate Leaian with a distinctly tuberculate dorsal carina. Neither the anterior nor the posterior carina is, however, tuberculated as in *L. leidyi* and growth lines are fewer than in *leidyi*. The Little River group is considered to be Permo-Carboniferous, or upper Devonian. Morphologically, *silurica* is a well developed Leaian, and the Leaiadidae are so far unrepresented in the Devonian fauna.

b. Lower Carboniferous of Europe

Euestheria tateana (JONES), England
Euestheria peachi (JONES), Scotland
Lioestheria striata (GOLDFUSS and MÜNSTER), Germany, Belgium, France, Scotland
Lioestheria youngi (JONES), Scotland
Asmussia tenuipectoralis (JONES), Kamensk, east of the Urals
Quadriasmussia hercynica (KUMMEROW), Germany
Leaia salteriana JONES, Scotland
Palaeolimnadiopsis jonesi RAYMOND, Scotland

Estheria striata tateana is recognized here as *Euestheria tateana* because of its reticulate sculpture. JONES' *tenuipectoralis* has an ovate carapace truncated by a long straight dorsal margin. Because the

posterior outline is not sinuated, its reference to *Palaeolimnadiopsis* is not tenable. Although JONES wrote that its umbo is terminal, its position, as suggested by three growth lines outside a smooth umbonal area, must be subcentral. For this reason *Asmussia* is suggested for this species. JONES' *Estheria dawsoni* from Scotland (1878) on which RAYMOND instituted *Palaeolimnadiopsis jonesi* has a sigmoidal posterior margin typical of *Palaeolimnadiopsis*. In *Lioestheria youngi* which is compared with the preceding the posterior outline is conspicuously truncated subvertically. The umbonal area appears to be smooth, possibly caused by erosion. Punctae are aligned in the interspace subvertically.

Finally *Estheria hercynica* which was found in the Kulm of Harz with marine shells lacks reticulation in the holotype, but it is found in other specimens from the same locality. The outline is unusually subquadrate, the small umbo elevated above the straight dorsal margin near its median point. As it is quite isolated from *Asmussia* or any other genera, *Quadriasmussia* is proposed for it.

Among the 8 species there is only one Leaian while a half of 6 Mississippian species belongs to *Leaia*, suggesting that it has not as yet developed in Europe.

c. Upper Carboniferous of Europe

The Upper Carboniferous Conchostracan fauna is a large one comprising 14 Estherian species, 5 Estheriellians and 17 Leaians, 36 species in all as listed below:

Euestheria beinertiana (JONES), Westphalian, England.
Euestheria cebenensis (GRAND'EURY), Westphalian, France and Russia.
Euestheria eleganta (CHERNYSHEV), Westphalian, Russia.
Euestheria rimosa (GOLDENBERG), Saarbrücken, Germany.
Euestheria tessellata (JONES), Coal Measures, Scotland.
Euestheria adamsi (JONES), Coal Measures, Wales.
Euestheria binneyana (JONES), Coal Measures, England.
Euestheria hauchecornei (FRITSCH), Stephanian, Germany.
Lioestheria striata (GOLDFUSS and MÜNSTER), Westphalian, Germany.
Lioestheria (?) *simoni* (PRUVOST), Westphalian, England, France, Russia.
Cyclestherioides (?) *nucula* (GOLDENBERG), Stephanian, Germany.
Estheriina (?) *freysteini* (GEINITZ), Westphalian, Germany.

Cornia chernyshevi (RAYMOND), Westphalian, Russia.
Cornia (?) *limbata* (GOLDENBERG), Stephanian, Germany.
Palaeolimnadiopsis pruvosti (RAYMOND), Westphalian, France, Belgium, Russia.
Anomalonema reumauxi (PRUVOST), Westphalian, France, Russia.
Anomalonema (?) *raricostata* (CHERNYSHEV), Westphalian, Russia.
Anomalonema (?) *densicostata* (CHERNYSHEV), Westphalian, Russia.
Anomalonema (?) *tegulata* (JONES), Coal Measures, Scotland.
Leaia rhenana HARTUNG, Namurian, Germany.
Leaia williamsoniana JONES, Westphalian, England.
Leaia bristolensis RAYMOND, Westphalian, England.
Leaia trigonoides MOYLEY, Westphalian, England.
Leaia boltoni RAYMOND, Westphalian, England.
Leaia minima PRUVOST, Westphalian, France.
Leaia raymondi KOBAYASHI, nov.=*Leaia pruvosti* RAYMOND, Westphalian, France, Belgium.
Leaia barroisi RAYMOND, Westphalian, Belgium.
Leaia subquadrata RAYMOND, Coal Measures, Wales.
Leaia paralella RAYMOND, Coal Measures, Wales.
Leaia cymrusensis RAYMOND, Coal Measures, Wales.
Leaia baentschiana BEYRICH, Stephanian, Germany.
Leaia herriana GUTHÖRL, Stephanian, Germany.
Leaia wettinensis LASPEYRES, Stephanian, Germany.
Paraleaia fritschi KOBAYASHI, nov., Stephanian, Germany.
Paraleaia klieveri (GOLDENBERG), Stephanian, Germany.
Paraleaia (?) *weissi* (FRITSCH), Stephanian, Germany.

Estheria striata beinertiana as well as *Estheria striata binneyana* are two *Euestheriae* with reticulation in the interspaces.

As suggested by its appellation, *Euestheria tessellata* has rectangular reticulae in which the concentric lines are stronger than the others. It is the type species of RAYMOND'S *Erisopsis*, but the type specimen in fig. 2 (JONES, 1891) is not much different from *Asmussia* except in its dense concentric lines. Because the valve in fig. 4a is unusually slender, it is improbable that its obliquity is due to secondary deformation.

GOLDENBERG'S *limbata* and *rimosa* resemble *Estherites* in the outline, but their umbones are located below the dorsal margin as in *Cornia*. As can be judged from JONES' reference of *limbata* to *Estheriina*, the umbo is elevated.

JONES (1897) included two forms in *Estheriina freysteini*. The one in fig. 10 is triangularly ovate; the other in fig. 9 is subcircular like *Cyclestherioides*. Both have straight dorsal margins and flattened peripheral bands which, however, are incomparably narrower than in typical *Estheriina*.

PRUVOST's group of *Estheriella reumauxi* is characterized not only by fine radial riblets but also by the sinuous posterior outline. The species was combined with KROTOW's *Estheriella trapezoidalis* and *E. oblongata* and WEISS' *Estheriella costata* in the group, but KROTOW's are pelecypods (LUTKEVICH, 1941), and WEISS' is the type of *Estheriella*. On the basis of PRUVOST's *reumauxi* RAYMOND established *Anomalonema*. CHERNYSHEV (1926) reported the occurrence of *Estheriella raricostata* and *Estheriella densicostata* beside *reumauxi* from the Donetz basin. His illustration is not clear enough to show the details of these species, but growth lines are evidently more numerous in *densicostata* than in *raricostata* and the two have very fine radial riblets. The specimen of *raricostata* in fig. 12, pl. 7 is a limnadiform and the intersections between the radials and concentrics are thickened as in *reumauxi*. As there is no Permian form linking *Estheriella* with the Carboniferous Estheriellians, *Anomalonema* is accepted here as a distinct genus.

Because *Dadaydedeesia* is invalid, *Estheria tegulata* is provisionally located in *Anomalonema*. Its sculpture is squarish and tile-like, the radial elements of which are different from those of *Estheriella*, as noticed by JONES. They appear to be grooves, instead of ridges in *reumauxi*. Concentric lines are very fine and densely distributed. The two illustrated specimens of the species are quite different in outline. The one in fig. 5 must be the holotype, because the other in fig. 6 a is said to be depressed, perhaps by pressure. The fineness of the radials is, however, a feature which can be seen in all these species.

One half of the Leaians listed above belong to RAYMOND's creation. Because *Leaia pruvosti* RAYMOND, 1946, is a homonym of *Leaia pruvosti* REED, 1929, a new name, *Leaia raymondi*, is proposed for RAYMOND's. I do this with pleasure as I recall his view on and criticism of my study on Cambro-Ordovician trilobites when I visited the Museum of Comparative Zoology in 1932 and 1933. *Leaia wettinensis* is, as noted by PRUVOST and RAYMOND, a remarkable species of *Hemicycloleaia* type showing a tendency to lose its radial carinae. The anterior carina is quite rudimentary. The posterior one in the

middle of the valve is cut by growth lines, indicated by a row of nodes. It may not be the true ancestor of *Monoleiolophus*, because there is a Pennsylvanian species which is much longer in outline. Incidentally, *Leaia wettinensis* is the largest *Leaia*, attaining 15 mm. in length and 11 mm. in height.

The radial groove in GOLDENBERG's *klieveri* is a very unusual feature. *Paraleaia* (?) *weissi* FRITSCH has a median fold between the anterior and posterior carinae. The fold, however, becomes stronger toward the venter, instead of dying out in the same direction as in *Paraleaia klieveri*. FRITSCH's *wettinensis* is different from LASPEYRES' not only in its broader outline but also in the posterior radials which are close set as in *Leaia curta*. Therefore FRITSCH's is called *Paraleaia fritschi*.

Besides these, *Leaia regis-ferdinandi* and *L. regis-borisi* which are similar to *L. minima* are reported from the Carboniferous of Bulgaria (PRANTL, 1939). In the Iberian peninsula *Euestheria cebenensis* and *Euestheria carneiroi* are found in the middle Stephanian of Northern Portugal (TEIXEIRA, 1943, '45). In its broad elliptical outline with a subcentral umbo the latter is a typical *Estherites*. *Leaia baentschiana* is reported to occur in the Westphalian of Leon in Spain (TEIXEIRA). In Morocco *Euestheria simoni* and *Leaia* cfr. *tricarinata* are reported from the Westphalian (TERMIER, 1950).

In closing this brief note on the Carboniferous Conchostraca of Europe, I should mention here that *Estheria punctatella* JONES from Scotland has been transferred into *Posidonomya*. Its shell grows as large as 32×22 mm. and is calcareous and pitted as in *Lepton* and *Kellia*.

4. Permo-Triassic Conchostracans in the Northern Continents

a. North America

A description of the subject may aptly begin with the Permian fauna of North America. Conchostracans are there restricted in their occurrence to the Lower Permian Wellington formation which is famous for its copious insect fauna. It is a non-marine sediment in a depression in front of the Arbuckle mountains. RAYMOND recently described the following 7 species.

Lioestheria raaschi RAYMOND
Lioestheria brevis (RAYMOND)
Lioestheria plicifera (RAYMOND)

Lioestheria rugosa (RAYMOND)
Cornia laminatus (RAYMOND)
Palaeolimnadiopsis carpenteri (RAYMOND)
Leaia reflexa (RAYMOND)

RAYMOND distinguished *plicifera* from *brevis* by the difference of 2 growth lines which, however, is possibly due to error in counting. Compared to them *L. rugosa* appears a little taller and its umbo has a more central position, but the holotype may be a little deformed. *L. raaschi* is said to be probably the form which used to be reported as *minuta* of Kansas and Oklahoma by some authors. In my opinion *brevis* and *plicifera* belong probably to the same species and possibly *raaschi* and *rugosa* to another. It is not improbable furthermore that the differences between *raaschi* and *brevis* are of sexual dimorphism. *Cornia laminata* is quite similar to them except in the presence of umbonal tubercle.

Palaeolimnadiopsis carpenteri, if really a Conchostracan, is the largest. In fact it attains 42 mm. in length and 28 mm. in height. Unfortunately, however, "all of the specimens are casts, showing no trace of the shell". Its peculiar preumbonal depression, concentric undulations and other aspects are not unlike *Anodonta*-like naiads. All others are no more than 7 mm. in length. I think it quite probable that the number of species would be reduced to a half or less, if a restudy were made on these Permian species.

In this continent there is a large break of Estherian record between the Lower Permian and Upper Triassic. The Newark series which is correlated to the Keuper is a filling of post-orogenic basins aligned in the axial metamorphosed zone of the Appalachian mountains from Nova Scotia to North Carolina through the Connecticut valley.

Posidonia ovata LEA from Pennsylvania and *Posidonia multicostata* EMMONS from North Carolina are two old Newark Estherians, both named in 1856. While JONES (1863) considered the two as belonging to the same species, they are distinguishable according to RAYMOND. Tuberculate *Estheria lewisi* (1890) and *E. hindei* with radial lirae (1891), both from Pennsylvania, were distinguished one from the other by JONES and *Lioestheria inornata* and *Pseudestheria emmonsi*, both from Virginia, by RAYMOND, all being from *ovata*.

These forms exclusive of *multicostata* and *lewisi*, but inclusive of WANNER's *Estheria mangaliensis pennsylvanicus* were combined in *ovata* by BOCK (1953) who noted that *ovata* is sexually dimorphic and the

inside sculpture polygonal tubercles, but the surface is finely reticulated. He is, however, not a simple lumper as can be seen from his description at the same time of *Isaura midothianensis* and *Howelllites winterpockensis* from Virginia, *H. princetonensis* from New Jersey, *H. berryi* from North Carolina and *Estheriellites ellipsoidea* from Pennsylvania. In the last species his *Estheriella circularis* and *E. ellipsoidea* (1946) are combined by dimorphic relation. This combination is questionable as discussed already on page 22. It is difficult for me to say how many good species there are in the above cited 13 species.

At all events there are some species of *Euestheria* and their taxonomic confusion depends in my opinion upon not only sexual difference but also to endemic variation as in the case of *Euestheria middendorfii*. I am especially interested in seeing polymorphism in the Newark Estherians which inhabited the post-orogenic basins aligned meridionally, because that is what I expect to find from my study of the Jehol Estherians. The savanna type of climate is sugested by KRYINE (1950) for the Connecticut valley in the Newark epoch. It may have been a little warmer in Pennsylvania and areas further to the south. Is it accidental that the largest of them is BOCK's species *princetonensis* from New Jersey and that Pennsylvanian *ovata* attains a similar size?

b. The Dyas and Trias basins

Estherians are found in some horizons from the Dyas to the Triassic.

Permian Estherians.

- *Euestheria muensteriana* (JONES and WOODWARD), Germany
- *Euestheria reinachii* (JONES and WOODWARD), Germany
- *Euestheria* (?) *geinitzi* (JONES and WOODWARD), Germany
- *Euestheria geinitzi* var. *grebeana* JONES and WOODWARD, Germany
- *Euestheria portlocki* JONES, England
- *Euestheria autunensis* RAYMOND, France
- *Lioestheria lallyensis* DEPÉRET and MAZERAN, France
- *Asmussia tenella* (BRONN), Germany
- *Cornia* (?) *drummi* (GUTHÖRL), Germany
- *Cornia* (?) *obenaueri* (GUTHÖRL), Germany

Thus there are 10 Permian species, mostly from the Rotliegende of Germany. GUTHÖRL's *drummi* and *obenaueri* are both allied also

to *Asmussia* in their submedian umbones on straight dorsal margins. Their centres are located below the dorsal margin. They appear very close to *Asmussia tenella*. JONES and WOODWARD's *geinitzi* and its var. *grebeana* are unusually tall and the latter is subtriangular. The former is nearer *Cyclestherioides* in outline.

In addition, *Estheria extuberculata* JONES and WOODWARD (1890) is described from Permian Stegocephalian limestone of Germany. It has a distinctly smaller umbonal area, like *Cornia*. Little is known of "*Estheria*" *rugosa* GÜMBEL from the Permian of Thuringia, but it is said to be similar to *tenella* and *exigua* in outline and to *middendorfii* in growth lines which are, however, more regular than in *middendorfii*. I have not as yet had the opportunity to see the description of "*Estheria*" *cyanea* FRITSCH from Bohemia. At any rate there is no Leaian in the Dyas fauna.

Conchostracans from the Triassic system of the German facies may be distributed into 10 or 11 forms, 6 of which are known from the Buntsandstein as follows:—

Euestheria alberti (VOLTZ)
Euestheria germari (BEYRICH)
Estheriella costata WEISS
Estheriella weissi PICARD
Estheriella lineata WEISS
Mesoleaia nodosocostata (GIEBEL)

As mentioned already, the type species of *Estheriella* is WEISS' *costata*, instead of *nodosocostata* which is distinct from *Estheriella*. They are small forms, *weissi*, 4.5 mm. being the longest. BEYRICH's *germari* resembles *Euestheria minuta*, but the longer dorsal margin of the former distinguishes it from the latter (BEYRICH, 1857). JONES (1891) illustrated *germari* with a carapace of a remarkably quadrate outline. This is quite different from *alberti* which PICARD (1911) synonymized with *germari*, because *alberti* has a semicircular outline. If *Estheria kubaczeki* VOLZ from the base of the Muschelkalk is really an Estherian, it may be an irregularly punctate *Lioestheria*, but its being a deformed *Posidonomya* appears to be not improbable.

Estheria minuta is a well known species of the Lettenkohle and the type of *Euestheria*. As pointed out by RAYMOND (1946), the species may be correctly credited to VON ZIETEN (1834) who was the first to illustrate it, because only the name is listed in the preceding publications (ALBERTI in DE LA BECHE 1832, and GOLDFUSS in ALBERTI, 1832).

Estheria minuta which PICARD (1911) described from the lower Keuper is quite circular in outline. Its umbo is central and distinctly protrudes above the short but straight dorsal margin. In fact it is intermediate in character between *Asmussia* and *Cyclestherioides* and very similar to *Cyclestherioides subcircularis* (RAYMOND). *Cyclestherioides picardi*, nov. is proposed for this form (PICARD, 1911, pl. 23, fig. 2). *Euestheria laxitecta* (SANDBERGER) is another important Estherian typical of the Gipskeuper. It is quite different from *minuta* in outline and number of growth lines. The former measures 10 mm. in length and 7 mm. in height. A Rhaetic variety of England, *Euestheria minuta brodieana*, was distinguished by JONES from the typical *minuta* by smaller polygons in the interspace. The occurrence of this variety in the Keuper of Upper Silessia is reported by ROEMER.

Incidentally *Estheria hausmanni* BEYRICH may not be an Estherian (KITTL, 1912). Carnic Estherians of Sicily described by SALINA must be restudied because they might turn out to be *Posidonomyas*, (see page 52). *Estheria loczyi* FRECH was procured from gray Estherian marl, a Cassianer equivalent, of Veszprim in Hungary. Whether it is an Estherian or whether it is a *Posidonia* or *Halobia* is an undecided question.

Farther south in the high Atlas of Morocco *Estheria destombesi* and (?) *Estheria minuta* are known to occur in the topmost of the five divisions of Triassic formation. As mentioned already, the latter does not coincide with German *minuta*, (see page 41). The former has a long subelliptical outline. Its umbo is located at a point one-third or one-fourth of the length from the fore part of the carapace. As no mention is made of its sculpture, it is provisionally referred to *Euestheria*. Its age is considered to be middle Keuper because *Equisetum mytharum* HEER was found in the same horizon. (DEFRETIN and FAUVELT, 1951)

c. Russia

Conchostracans greatly developed in Russia in the Tatarian, but died out after the Vetlugian. According to LUTKEVICH (1941) KROTOW's *Estheria* and *Estheriella* are calcareous shells of pelecypods. The oldest among the Permian Estherians in Russia is *Estherites mezensis* (LUTKEVICH) from the Lower Permian red beds on the Mezen river. Its test is punctate. Three punctate forms are known from the Kazanian as follows:

Euestheria eichwaldi (NETSCHAJEW) from the Kazanian of the Kargala mines.

Cyclestherioides exigua (EICHWALD) from the Kazanian from the South Urals to the western slope of Timan.

Leaia kargalensis NETSCHAJEW from the Kazanian on the Kama river.

EICHWALD's *Cyclas eos* was synonymized with his *exigua* by JONES (1862). The subcircular outline and median umbo suggest *Cyclestherioides* as the holotype of *exigua*. As LUTKEVICH's *exigua* is quite different from it in the subovate carapace and terminal umbo, *Lioestheria lutkevichi*, nov. is proposed on the basis of the specimen in fig. 6, pl. 1 (LUTKEVICH, 1941).

The groove in *eichwaldi* pointed out by NETSCHAJEW which extends from the beak to the postero-ventral margin is said to be accidental, because the specimens are secondarily flattened. Its sculpture is polygonal, instead of granular. *Leaia kargalensis* has only two carinae, but these carinae as well as the dorsal margin are thickened into nodes at intersections with growth lines.

The Conchostraca developed suddenly in the Tatarian in which 10 species in 5 genera can be distinguished as follows:

Lioestheria elongata (NETSCHAJEW) from the North Dvina beds.

Lioestheria trapezoidalis (NETSCHAJEW) from the North Dvina beds and the Tatarian of the Volga.

Lioestheria angulata (LUTKEVICH) from the North Dvina beds.

Lioestheria lineata (LUTKEVICH) from the North Dvina beds.

Lioestheria cellulata (LUTKEVICH) from the North Dvina beds.

Lioestheria rotunda (LUTKEVICH) from the North Dvina beds.

Estherites kobozevi (LUTKEVICH) from the Fileyskoe beds of the Entala river.

Cornia melliculum LUTKEVICH from the Fileyskoe beds.

Vertexia tauricornis LUTKEVICH from the Fileyskoe beds.

Monoleiolophus monocarinata (LUTKEVICH) from the Tatarian of the Vetluga river.

They are all small forms less than 4.5 mm. in length and all have punctate tests. In *cellulata* and *rotunda* the punctae are complicated by cellular depressions between the growth lines. The sculpture is thought to be intermediate between punctation and polygonal reticulation. In *Estherites kobozevi* the umbo is located in the middle part of the dorsal margin. Its carapace is subovate, 3 mm. long and 2 mm.

high. *Cornia melliculum* is the smallest, 2 mm. long and 1.8 mm. high. Other small ones are *Vertexia tauricornis*, 12.5 mm. long and *Monoleiolophus monocarinata*, 2.3 mm. long. A carina of the last species is tuberculate at the intersection with the growth lines and their interspace is coarsely punctate.

The largest among these Permian Estherians is *Euestheria eichwaldi*, 8 mm. long and 6.8 mm. high. The next is *Estherites mezensis*, 5 mm. long and 3.8 mm. high. The length and height of *Leaia kargalensis* is 6.7 mm and 4.5 mm. respectively. Growth lines do not exceed 20 in these Permian Conchostracans. The vertical distribution of the 16 Permian species reveals acceleration in the Conchostracan development through the Permian period, but the group shows a decline after the Permian. The Tatarian in the old sense is now divided into the Tatarian proper and the Vetlugian which yields

Lioestheria gutta (LUTKEVICH)
Lioestheria aquale (LUTKEVICH)

d. Siberia

As I have alluded briefly to *Euestheria karpinskiana* from the Rhaetic (?) of the east Urals, (see p. 40), let us examine the Kuznetsk basin. A Carboniferous Estherian is reported from the right bank of the Tom river in the Kuznetsk basin by INOSTRANZEW and DESHWIN (OBRUTSCHEW, 1926). Was it the same species as *Cornia papillaria* from the Upper Permian Kolchugino series on the right bank of the same river at the top of Baby Kamen?

Praeleaia triassiana, the monotype of *Metaleaia*, is found in the Maltsévo series along the Tom, Tersy, Chernavi and Narwick rivers in the basin in association with *Cyclestherioides subcircularis* and *E. minuta* (?) CHERNYSHEV, 1934, for which a new name, *Lioestheria pseudominuta*, is given, (see page 40). Later Vetlugian *gutta* and *aeguale* were found in the Maltsévo (LUTKEVICH, 1937). Though the series was previously thought to be Upper Triassic, it is certainly Lower Triassic. There is neither any distinct discordance nor any conglomerate at the base. The Pfaelzian phase of deformation must have thus been slight in the basin. The conglomerate series on the contrary is a post-orogenic type of sediment lying on older formations with a remarkable discordance and the flora contained in it belongs to the Mine group rather than to the Toyora (Dogger-Neocomian) group. Therefore the age of this flora must be in a range from late

Triassic to early Jurassic. Accordingly it is probable that the principal phase of deformation in the Kuznetsk basin is possibly Middle Triassic. This conclusion necessitates a reexamination of deformation in this general region. The Akiyoshi orogeny may not have been weak in Central Asia because Triassic discordance is expected by WJALOW (1937) to be strong and extensive there.

As noted in the preceding chapter, (see page 67), Central Asia is a promising field for hunting fossil Estherians, although little has been done in the way of study. In the Upper Tungussian Korvunchansk stage on the upper Tungusska in Central Siberia *Estherites tungussensis* and *Estherites* (?) *venekiensis* are found in association with *gutta, aquale* and *subcircularis* (LUTKEVICH, 1938). Besides these this stage contains gastropods and ostracodes, but the gastropods bear no resemblance to Permian ones in Russia and the ostracodes are also distinct from the Permian ones in Tatar and the Kuznetsk basin, but closely allied to the early Triassic ones in Leningrad and Volga regions.

A rich Permian Estherian fauna comprising 15 species was found in bore cores of drills on the shore of the Chatanga bay and 16 forms were distinguished by NOVOZHILOV (1946). He erected *Polygrapta* on the basis of *Polygrapta chatangensis* and referred 8 species to the genus and the remaining 7 were placed in *Estheria*. The distinguishing characteristic of the genus is in the sculpture in the interspaces which is composed of chains of granules aligned radially. The sculpture in other words is a kind of radial lirae which are sometimes branching. He considers the phylogenetical relation of *Polygrapta* to *Estheriella* to be close, but the rows of granules never cross the growth lines.

As *Polygrapta ignota* is said to be very similar to three species of *Cornia* (*papillaria, mellicum* and *ortoni*), its reference to the genus is suggested, although its illustration is not clear enough to enable one to ascertain the characteristic umbonal aspect. As *Polygrapta limbata* is said to have a small umbonal swelling, it might be another *Corina*. His *Estheria trapezoidalis*, especially the one in fig. 7 and *Estheria ventriculita* are a typical *Asmussia*. The faunal list is emended as below:

Euestheria chatangensis (NOVOZHILOV) (No. 1 in fig. 6)
Euestheria strictocostata (NOVOZHILOV) (No. 2)
Euestheria multinstita (NOVOZHILOV) (No. 3)
Euestheria necta (NOVOZHILOV) (No. 4)

Euestheria laxa (NOVOZHILOV) (No. 5)
Euestheria laptewi (NOVOZHILOV) (No. 6)
Euestheria intaminata (NOVOZHILOV) (No. 7)
Euestheria cicatricosta (NOVOZHILOV) (No. 8)
Euestheria toricata (NOVOZHILOV) (No. 9)
Euestheria petasa (NOVOZHILOV) (No. 10)
Lioestheria nordvikensis (NOVOZHILOV) (No. 11)
Lioestheria aequale var. *arguta* (NOVOZHILOV) (No. 12)
Lioestheria trapezoidalis (NETSCHAJEW) (No. 13)
Asmussia ventriculita (NOVOZHILOV) (No. 14)
Cornia (?) *ignota* (NOVOZHILOV) (No. 15)
Cornia (?) *limbata* (NOVOZHILOV) (No. 16)

As noted elsewhere (see page 43), all of the Estherians are small. Growth lines number some 30 in *Euestheria strictocostata* and *E. multinstita* but others have less than 20.

An Anisic fauna was found in cores of drills in the region of the Tiguian river, a left branch of the Anabar river near the Tschaidakh lake. Estherians are contained in an argillaceous layer within dark green sandstone. In addition, *Lingula tenuissima* BRONN, *L.* cfr. *polaris* LUNDGR., *Lingula* sp., *Gervillia arctica* KIPARISOVA and *Trigonodus praelongus* KIPARISOVA and *T. serianus* KIPARISOVA are contained in the beds. Therefore they are presumed to be brackish sediments, as a deltic condition was suggested by NOVOZHILOV (1946).

From the Anabar collection he described 7 species. *Diaplexa* and *Diaphora* are his two new subgenera of *Estheria* and *Diaplexa tigjanensis* and *Diaphora tuberculata* are the respective monotypic species. The former is a triangularly ovate carapace. On the surface there are irregular wrinkle-like crests crossing the growth lines. It is questionable whether the wrinkles are primary or secondary. As their interspace is granulated, it is placed in *Lioestheria*. The latter species has a semi-ovate carapace and a subterminal umbo. The sculpture of the interspace consists of large tubercles of various sizes on which granules are scattered. Judging from his description, the sculpture seems to me to be more likely of the *orientalis* type than the *chinensis* type. Therefore it is tentatively referred to *Lioestheria*. *Estheria deverta* has an elliptical outline and subcentral umbo typical of *Estherites*. It resembles *Estherites naktongensis* but is taller and test is granulated.

Euestheria exsecta (NOVOZHILOV) (see figure 6, a)

Euestheria meta (Novozhilov) (b)
Lioestheria tigjanensis (Novozhilov) (c)
Lioestheria tuberculata (Novozhilov) (d)
Lioestheria anabarensis (Novozhilov) (e)
Lioestheria nodosa (Novozhilov) (f)
Estherites deverta (Novozhilov) (g)

The Estherians in 7 species are all small; smaller than the Permian ones of the same regions on the average. The growth lines are less in number, 17 in *Estherites deverta* being the maximum.

5. The Gondwana Conchostracans

In peninsular India there are two old species of Jones known by the following names:

Euestheria mangaliensis (Jones) from the Permo-Triassic Damuda formation,

Euestheria kotahensis (Jones) from the Jurassic (?) of Kota.

So far as I am aware, no addition has since been made from the Gondwana system.

a. Africa

The oldest known species in Africa is *Estheria greyi* Jones, 1878, procured from the vicinity of Cradock, Cape Colony, South Africa, in the upper Karroo formation which is now considered a middle or upper member of the Beaufort. Because the center of the smooth umbo lies below the dorsal margin, it may be a *Cornia*. The interspace appears smooth except for radial wrinkles which were thought to be secondary products by the describer. Jones and Woodward's *Estheria draperi* and *E. stowiana*, 1894, from the upper Karroo, are known now to be wide-spread in the upper Triassic Cave sandstone. The two are so similar as to belong to the same species; *draperi* has a submedian umbo and coarse pits forming an obscure reticulation and was selected by Raymond for the type of *Orthothemos* which I consider to be a synonym of *Estherites*.

Marlière (1950) compiled a correlation table showing distribution of non-marine invertebrates in the Karroo system. As I have no opinion on the geology of this continent, I shall follow this table.

Estheria borgesi Teixeira, 1943, from the plant-bearing Grés de Tate in Mozambique is a Stephanian or Permian *Euestheria* resembling

Euestheria rimosa. *Estheria* (*Pemphicyclus*) *gabonensis* MARLIÈRE, 1950, from Zambezie is a typical *Cornia* of similar age.

Leaia sp. occurs in the lower Beaufort (Upper Permian), but is as yet undescribed; *Euestheria anchietai* (TEIXEIRA) from the Upper Permian Cassanje I in Angola, according to the author, resembles *Palaeestheria lebombensis* RENNIE from the Lias of the Lebombo range between Transvaal and Portuguese East Africa. The former looks to me like an *Estherites* similar or ancestral to *E. grayi*.

Estheriella nyasana NEWTON from Nkana, Nyasa, is such an aberrant form that *Nyasestheriella* is proposed for it. (See page 33). Its age is said to be Permo-Carboniferous Karroo, but its true age is still indefinite.

The late Permian Lualaba I formation in the Congo basin is a correlative of the Cassanje I and yields

Euestheria passani MARLIÈRE, 1950.
Euestheria sp. nov.
cfr. *Euestheria minuta* by MARLIÈRE, 1950.
Estheriella lualabensis LERICHE, 1931.

The radial ribs of the last species are thickened into a series of nodes and interrupted by growth lines. This ornamentation and the ovate convex carapace are the characteristics of *Congestheriella* which is erected for this species.

From the Lower Triassic Lualaba II formation or the Ètage de la Loia are known *Euestheria kasaiensis* MARLIÈRE and *Euestheria minuta* var. *brodiei*. The latter may be a distinct species from JONES' *brodieana*. Estherians occur in the Groupe de la Sakamera, both in les schistes à plantes and les schistes à reptiles and in the Red Beds in Madagascar (BESAIRE, 1952), but the Conchostracans appear to have declined for some time after the Permian.

In the Upper Triassic Kwango I formation in the Congo basin is found *Euestheria angolensis*. In addition some others are known from its equivalent formation i.e. the Cassanje III in Angola and they are

Euestheria angolensis (LERICHE)=*Euestheria lerichei* MARLIÈRE, 1950.
Euestheria malangensis MARLIÈRE, 1950.
Echinestheria marimbensis MARLIÈRE, 1950.
"*Estheriella*" *moutai* LERICHE, 1932.

In 1932 LERICHE described *Estheriella moutai*, and *Estheria mangaliensis* var. *angolensis* from northern Angola. The former is

similar to German *Estheriella* but their radial ribs are much stronger. In the collection from Quela cliffs TEIXEIRA (1947) ignored the variety *angolensis* and noted the polymorphism of *mangaliensis*. MARLIÈRE (1948) however accepted var. *angolensis* as a distinct species, *lerichei*, and showed the morphic change of his *malangensis* through growth. To me it is interesting to find that *angolensis* in the Congo and Angola basins reveals extensive morphic diversity like *Euestheria middendorfii* in the Jehol basins in Eastern Asia.

Euestheria draperi is reported from the Cave sandstone of the Stromberg series and *Cyzicus* sp. (*Euestheria* sp.?) from the Lubilash beds at Kitari, Cañon of Inzia, Belgium Congo (HAUGHTON).

"*Estheriella*" *bornhardti* from a green sandstone of Mkumbi, southeast of Kissaki, comprises two forms, i.e. the minor one of about 3 mm. or less in length and the major one of 6 to 7.5 mm. in length. The holotype (No. 13) is a major form, roundly subquadrate. The dorsal margin is straight; umbo smooth; fine radial ridges on the posterior side form tiny nodes with concentric lines at their intersections.

The Maji ya Chumvi beds of the Triassic Duruma sandstone on the Uganda railway in British East Africa yield Estherians (MUFF). An undescribed *Estheriella* (?) is reported to occur in north Adamana (DIETRICH, 1939). Purbekian *Euestheria tendagurensis* and *Cyclestherioides janenschi*, and *Lioestheria anomala* (JONES) from the Lower Cretaceous Enon conglomerate of South Africa are the post-Triassic representatives on this continent. JONES' *anomala* (1901) comprises two or more forms. One in text-fig. 1 is much longer than the two others in text-figs. 2 and 3. Thus there are some 24 species, namely 9 Permo-Carboniferous, 11 Triassic and 4 later Mesozoic.

b. South America

In Brazil there are at least three Conchostracan faunas. The oldest from the *Série de Passa Dois* yields the following;

Estherites regularis (REED)
Estherites regularis var. *multistriata* REED
Estherites neotropica (REED)
Palaeolimnadiopsis subalata (REED)
Leaia pruvosti REED
Bileaia curta (REED)
Monoleiolophus unicostatus (REED)

The largest is the fourth, 9 mm. long and 6 mm. high. It is noted that *Estherites regularis* has "interspaces with concentric striation and internally minutely pitted". The interspace is minutely granulated in *Leaia pruvosti* and regularly reticulate and the concentric lines of growth run over the flat topped radial ribs in *Monoleiolophus unicostatus*. *Bileaia curta* is an aberrant form having two carinae on the posterior and possibly one on the anterior side (REED, 1929). This unusual form is distinguished from *Leaia* s. str. as *Bileaia*. The age of the fauna is generally considered to be late Permian (ALMEIDA, 1952, MAACK, 1952).

Besides these there is *Acantholeaia regoi* (ALMEIDA, 1950) from the Permian in the state of Sao Paulo which is a unique tricarinate form with a row of spines on the subdorsal carina.

The next oldest is a faunule from the *Série de Sao Bento* (ALMEIDA, 1950) comprising

Euestheria mendesi ALMEIDA
Euestheria barbosai (ALMEIDA)
Estheriina petrii (ALMEIDA)

and its age is either Rhaetic or Rhaeto-Liassic (ALMEIDA, BARBOSA, MENDES 1952).

The third is the Bahian or Neocomian one (GERTH, 1935) which consists of *Euestheria mawsoni* and three species of *Estheriina* i.e. *bresiliensis*, *expansa* and *asteroides*, the first being the type of the genus (JONES, 1890, 1897).

Thus the Brazilian Conchostracan fauna, 15 species in total, consists of 8 Permian, 3 Triassic and 4 Cretaceous species.

As shown in JONES' excellent review (1897), Estherians have long been known to occur in Argentina, Peru and Chili. Through a revision on GEINITZ's (1876) and PHILLIPI's (1887) works in addition to a study on FORBES' collection (JONES, 1862), JONES recognized the following 4 species;

Estheria mangaliensis JONES (=GEINITZ's *E. mangaliensis*, pars) from Mendoza in Argentina.
Estheria forbesii JONES (=*E. mendosiana* PHILLIPI, *E. mangaliensis* GEINITZ, pars) from Mendoza in Argentina.
Estheria aricensis JONES from Arica in South Peru.
Estheria chilensis PHILLIPI from Lebu (?), Chili and Arica of South Peru.

Reticulate *forbesi* and also the so-called *mangaliensis* from the Rhaetic (?) of Mendoza belong to *Euestheria*. *Euestheria aricensis* has unbranching radial lirae which, however, never cross the growth lines. RAYMOND erected *Pseudestheria molesta* for JONES' *chilensis* in fig. 4, but as noted by JONES, the resemblance of *chilensis* inclusive of *molesta* to *Cyclestheria* is certainly remarkable. Therefore *Cyclestherioides* is a better position for them than invalid *Dadaydedeesia* or *Limnadopsis*. The geological age of the species from Peru and Chili is unknown.

GEINITZ noted that Estherians are common in the *Brandschiefer* near Mendoza. Lately RUSCONI (1947, '48) amplified the Triassic or Rhaeto-Liassic Estherian fauna of the province. *Pseudestheria contorta* and *P. leonensis* are two *Cycloestherioides*. His *Estheria* (*Pseudestheria*) *minoprioi* is a peculiar form having the growth band more steeply inclined on the umbonal side than on the peripheral side. Its strong undulations remind one of *Rhabdostichus*. *Estheriopsis bayensis* has a linguloid outline with radial ribs divergent from the umbo. Its reference to the Lioestheriidae or even to the Conchostraca needs further confirmation. *Euestheria striolatissima* is, however, a normal form of the genus.

Figure 24.
Estheriopsis bayensis RUSCONI ×3

Recently BOCK (1953) described *Isaura olsoni* and *Howellites colombianus* respectively from the Rhaetic (or Liassic) near Merida in Venezuela and from a shale of similar age near Montebel, Columbia. The former appears to be an *Euestheria* and the latter may also be another *Euestheria*.

Thus some 10 species of Estherians are distributed in the Andes from Venezuela to Mendoza of Argentina, most of which are contained in the Triassic, and two are of unknown age.

c. Australia

The Estherian occurrence in the Moore Park Diamond Drill bore was announced by COX as early as in 1881. *Estheria coghlani* was its name, and was later adopted by ETHERIDGE in its description (1888). ETHERIDGE reported also the occurrence of *E. mangaliensis* in the Denmark Hill shale near Ipswich, Queensland and *Leaia mitchelli* near Belmont in New South Wales (1892). The prolific fauna of Eastern Australia was not, however, uncovered until two papers by

Mitchell came out (1925, '27). In the earlier paper he showed a great variety of Leaians including quadricarinate and discoidal forms. Beside *L. compta* from the Dirty coal seam, more than 13 species of Leaians were found in a thin layer half an inch thick which is an intercalation in the Belmont beds. Besides Estherians the layer yielded insects, plants and other fossils. The Upper Permian Conchostracans in New South Wales are listed below.

Euestheria novocastrensis (Mitchell)
Euestheria trigonellaris (Mitchell)
Euestheria obliqua (Mitchell)
Euestheria lata (Mitchell)
Lioestheria bellambiensis (Mitchell)
Lioestheria (?) *belmontensis* (Mitchell)
Cyclestherioides lenticularis (Mitchell)
Estheriina glabra (Mitchell)
Estheriina linguiformis (Mitchell)
Discoleaia discoidea (Mitchell)
Quadrileaia quadricarinata (Mitchell)
Trileaia mitchelli (Etheridge)
Trileaia intermedia (Mitchell)
Trileaia belmontensis (Mitchell)
Trileaia sulcata Kobayashi (nov.)
Trileaia etheridgei Kobayashi (nov.)
Monoleiolophus (?) sp. indet.
Leaia oblongata Mitchell
Leaia paraleidyi Mitchell
Leaia pincombei Mitchell
Leaia elliptica Mitchell
Leaia ovata Mitchell
Leaia latissima Mitchel
Leaia compta Mitchell
Leaia collinsi Mitchell
Leaia quadrata Mitchell

Trileaia intermedia has, besides two primary radial carinae, a secondary radial which is located in the posterior section, instead of in the middle in *L.* (*P.*) *klieveri*. *Trileaia sulcata* (nov.) is proposed for Mitchell's *Leaia* sp. indt. (p. 446, pl. 43. fig. 20). It disagrees with *intermedia* in its more elliptical outline, its longer posterior groove closer to the dorsal margin and abrupt obsoletion of two

carinae at a short distance from the ventral margin. *Leaia discoidea* is a bicarinate form whose outline is totally different from that of all Leaians. This species represents *Discoleaia*, a new genus by itself. The holotype is in fig. 6, pl. 41 and the paratype in fig. 22, pl. 42. The latter probably shows the original outline.

Leaia quadricarinata has a contour similar to *L. mitchelli*, but also two short extra-radials close to the dorsal and anterior margins. *Quadrileaia* is proposed for it. In *Leaia latissima* two radial carinae die out in some distance from the ventral periphery. Aside from the dorsal carina, the three others radiate regularly on the valve of *Leaia belmontensis*. Its outline looks more hemicycloid than any of RAYMOND'S *Hemicycloleaia*. *Trileaia* is instituted on this species. On first glance it resembles *Mesoleaia nodosocostata*. There is one more quadricarinate form (p. 446, pl. 43, fig. 21) which can easily be distinguished from *belmontensis* by its broad outline. *Trileaia etheridgei* is proposed for it. *L. intermedia*, 10 mm. long and 7.5 mm. high, is the largest and *L. oblongata* 11 mm. long and 3.9 mm. tall is the longest, *L. latissima* 8.8 mm. high and 6.7 mm. long has the greatest height relative to length.

Among the three Estherian species from the same chert only a few concentrics are shown in *C. lenticularis*, but others are said to be seen with a magnifer. *E. glabra* and *E. linguiformis* may be referable to *Estheriina*. It is questionable whether the subdorsal flattening of *E. belmontensis* noted by MITCTELL is primary or secondary. Otherwise it is a *Lioestheria*, if not an *Euestheria*. If *E. bellambiensis* procured from a horizon near the preceding, has sculpture like *E. striata*, it must be another *Lioestheria*, instead of an *Unionella*. This is the largest Estherian in Australia, measuring 10 mm. in length and 6 mm. in height.

A greater variety of Estherians including *Cyclestherioides lenticularis* is found in the collection from a horizon a few feet below the Dirty coal seam. The above mentioned species is a small form only 2 mm. long and 1.8 mm. high. Because the sculpture of the four others is unknown (*novocastrensis*, *trigonellaris*, *obliqua* and *lata*), they are provisionally located in *Euestheria*.

Thus the fauna of the Upper Permian Newcastle coal measures comprises 8 Estherian species and 16 or more Leains some of which are quite abnormal. High specialization and dwarfing owing to severe climate are noted by TILLYARD for the Upper Permian insect fauna

of Australia. Chert from the Belmont quarries which yields insects, Conchostracans and others is volcanic dust or very finely divided particles of devitrified rhyolitic tuff in origin. According to MITCHELL, Conchostracans were imbedded in the Belmont beds by a sudden drying up of the water, aided by falling ashes. This was an episode in the Kamilaroi period. Because the Newcastle coal measures are spread transgressively over the upper marine series and contain reworked material of the Greta coal measures, Conchostracans were inhabitants in the depressions introduced by this phase of deformation, after the Bolwarra glaciation (DAVID, 1932).

The Permian period came to a close in New South Wales without any strong disturbance save a broad warping through which the Triassic Cumberland basin was produced. The base of the Triassic system is marked off by Estherian shale. *Euestheria* (?) *coghlani* is, however, a *Dauerfossil*, occurring in the Narabeen (DAVID, 1932), the Howkesbury (CHAPMAN, 1914) and the Wianamatta series, the last of which yields in addition, *E. wianamattensis* and *E. glenleensis*. The former, the type of RAYMOND'S *Palaeolimnadia*, is 3 mm. long and 2 mm. high and referred here to *Estherites*. The latter is an *Estheriina*, 4 mm. long and 3 mm. high.

Orogeny probably did not cease until the middle Triassic period in Queensland where the Ipswich coal-measures lie clino-unconformably on the upper Bowen coal-measures (DAVID, 1932, KOBAYASHI, 1949). This post-orogenic sediment contains *Estheria ipsviciensis*, which is ETHERIDGE'S *mangaliensis* and may be an *Euestheria*. This is the largest among these Triassic species. It is, however, only 6 mm. in length and 5 mm. in height.

It is certainly a remarkable fact that Conchostracans developed sporadically in the late Permian in Australia. They declined in the Triassic period. Not only in the maximum size of the carapace but also in the number of species, the late Permian fauna is far superior to the Triassic one.

In closing this chapter I must not overlook the occurrence of *Estheria minuta* (?) in New Zealand (page 41) as an item in the faunal list of Australasia. The source of CHAPMAN'S statement is probably PARK'S (1904) or THOMSON'S (1913) paper. The so-called *minuta* is cited in the faunal list of the *Trigonia* beds which are now considered to be probably an Oretian member. It may be a juvenile *Halobia* according to FLEMING. (Personal correspondence from Prof. BENSON).

CHAPTER V

The Rise and Fall of the Conchostraca

1. The increase in the number of species and genera

When JONES (1863) discussed the distribution of fossil Estheriae, he enumerated 14 species and 6 varieties of *Estheria* and 1 species and 2 varieties of *Leaia*. RAYMOND (1946) classified some 150 forms into 20 genera. Besides these there were 12 genera before this revision. I am inclined to be more conservative than RAYMOND in accepting Estherian genera because of their morphic obscurity, but more progressive in the case of Leaians and Estheriellians because there are so many aberrant forms which cannot be kept in *Leaia* or *Estheriella*. I have therefore resolved to establish 8 new genera all having radial markings. *Quadriasmussia* is the only new Estherian genus which is added on this occasion.

Through this study I found some 300 forms. As the number has increased thirteen times in the 90 years since 1863, it may well increase some fifteen times in a century. In fact only 5 species had been described from 4 localities in the vast terrain involving Japan, Korea and Manchuria, when I commenced the study of this field. A large number of species will undoubtedly be found in the future in Central Asia and southern continents.

The number of species and of genera differ of course quite widely as between a splitter and a lumper, as pointed out already (page 95). The difference is especially great in polymorphic species which are generally found in intra-continental basins. The number of Estherians may be reduced, if the classification is made merely on the basis of morphology, because it may happen that a Carboniferous species in England is almost identical with a Triassic species in Australia. It is known, however, that the distribution of living Estherians is mostly restricted. Therefore the Estherian species in the past must have been local or regional. It can be expected, in view of *Limnestheria ardra*, for the body to differ no less when time is different.

For the time being the classification of Estherians is artificial, because little is known of the soft body, the biological bearing of the outline of the carapace, the sculpture in the interspace, tubercles in the umbonal area and so forth by which distinction is made. It is

inevitable at present that Estherians should be classified into form-genera, unless all of them are to be left in a dumping ground. Their family-reference is also very tentative.

The classification of the Conchostraca with radial markings is easier. As a result of this study on Estheriellans I arrived at the conclusion that generic distinction is fairly clear, but the Estheriellidae are a form-family for taxonomy. The Leaiadidae are on the contrary a monophyletic family, instead of polyphletic as thought by RAYMOND, and the evolutional trends of Leaians are now fairly well understood.

In this paper non-marine Conchostracans are distributed in 28 genera in 5 families and their specio-temporal distribution is figured out in the preceding two chapters. Starting from the shifting of the center of distribution, morphic radiance and its relation to the earth movement is discussed in this chapter. Then consideration is extended to phylogenetic relation among the genera and families and their ancestors and descendants.

2. The shifting of the center of distribution

Ignoring a little known Burmese form, all 17 species of the Devonian Conchostracans are distributed in the Old Red *Gürtel* or Eur-America, where *Asmussia* was well developed and the Estheriellidae were represented by the two Middle Devonian species of *Praeleaia*.

In the early Carboniferous period distribution did not change much but specific number was reduced to 16. The reduction, however, means that on the European side and on the North American side the number increased from one Devonian to 6 Mississippian species which thrived exclusively in Acadia. The sudden development of the Conchostraca in the early Carboniferous in Nova Scotia may be said to be an after effect of the Acadian disturbance which came *en retard* after the paroxysm of the Caledonian orogenic cycle because they are inhabitants in the post-orogenic basins.

There were two *Eoleaias* besides an indeterminable Leaian in North America, while in Europe *Leaia salteriana* in Scotland was the solitary member of the Leaiadidae. In 10 Pennsylvanian species 6 belong to *Leaia* and one to *Monoleiolophus*. Except two species in the Illinois basin, all of them are distributed in the Appalachians (Pennsylvania, Rhode Island and Ohio).

On the European side of the *Kohlengürtel* the Conchostraca

reached the climax of development in the Upper Carboniferous, when there were some 40 species. Leaians are well represented by more than 15 species. *Paraleaia* is an aberrant genus in the Stephanian. *Anomalonema* is a characteristic Estheriellian genus, which is by no means related to *Praeleaia*. It is a remarkable fact that non-marine Conchostracans have developed parallel to land plants. As for most other geobios and limnobios, they flourished on land and in the basins introduced by orogeny. It is a general tendency for morphic diversity to be higher in the synorogenic isolate basins than in the large late orogenic or post-orogenic basin behind the mountains.

Some 10 species of Estherians are known from the Dyas. There was no Leaian nor any Estheriellian, but one *Leaia* is included in a few Lower Permian Conchostracans of Oklahoma. The world-wide distribution of the Conchostraca in the Permian period is an important event in their history. Their wide dispersal had already started in the latter part of the Carboniferous. In fact one Estherian species is known from the Upper Carboniferous of North China and one or two of Mozambique and Zambezie in South East Africa may be Stephanian, if not Permian. The Lower Carboniferous *tenuipectoralis* from Kamensk, east of the Ural and some other Westphalian ones in the Atlas in North Africa indicate the first step. Dispersal to remote places must have been accomplished by the repeated transportation of egg-capsules from one basin to another.

Broadly speaking, the Conchostraca developed much more in the latter than in the earlier part of the Permian period, although the reverse was the case in the Dyas basin in Europe. In Russia there is only one species in the Lower Permian. The number of species becomes 5 in the Kazanian and 10 in the Tatarian. In central Siberia one is known from the Kolchugino and 15 from the Chatanga basin. At the time Northern Eurasia was the center of distribution in northern continents.

On the side of Gondwana late Permian Conchostracans thrived in the Congo-Angola basin (5 species), Brazil (8 species) and in New South Wales where the fauna was most copious, comprising 26 species in 9 genera. Morphic radiance of the Leaiadidae attained the climax in the late Permian when peculiar *Bileaia*, *Trileaia*, *Quadrileaia*, *Discoleaia* and *Acantholeaia* appeared. They as a whole indicate maximum divergence in the phylogerontic stage, and the family died out at the end of the Palaeozoic era, leaving *Mesoleaia* as a solitary

relict. *Vertexia* is an aberrant Estherian genus which appeared simultaneously in the Tatarian basin.

In the Triassic period Estherians declined in the southern continents, but developed somewhat in the late Triassic or Rhaeto-Liassic epoch where 9 species are known from the Angola, Congo and other basins of Africa, 2 from the Atlas, 3 from Brazil, 3 from Eastern Australia and 8 from the Andes. In Germany there are 6 species from the Buntsandstein inclusive of the basal Muschelkalk. Vetlugian *gutta* and *aequale* occur in the Maltsévo of the Kuznetsk basin and also in the Upper Tungussian of central Siberia where the Maltsévo and upper Tungussian each comprises 5 species and *Lioestheria subcircularis* is common between the two. The 7 Anisic Estherians are, however, all indigenous to the Anabar basin in Northern Siberia. *Euestheria karpinskiana* is known from the Rhaetic of the Eastern Urals. Further west 4 forms are known from the Keuper inclusive of the Rhaetic.

The sporadical appearance and disappearance of *Estheriella* and similar African forms in addition to isolate *Metaleaia* and *Mesoleaia* are remarkable. Whether or not these Estheriellians in the northern and southern continents are really related is indefinite. From the Newark series in eastern North America 13 species were distinguished, but these may turn out to be a few polymorphic species. Under such circumstances it is difficult to count the number of species, but there may have been some 50 forms in the whole Triassic, even if the Asiatic ones of this age are excluded. Two-thirds of them are Upper Triassic or Rhaeto-Liassic.

A few Estherian relic forms are found in these continents. More precisely, 2 species from Dogger and 3 from Neocomian are known in Europe, a Jurassic one in India, 3 Neocomian ones in Africa and 4 Neocomian ones in Brazil beside 3 indeterminable forms from the Jurassic of Louisiana. Namely, 13 to 16 species in all are those known outside Eastern Asia where on the other hand Estherians developed greatly after the Ladinic epoch. There are in fact 48 species, 6 varieties and 4 formae, as shown in the table VIII.

The rise and fall of non-marine fossil Conchostraca indicated by the number of their forms are shown in figure 25. They as a whole reached their climax in the Permian period when 83 forms in 17 genera existed. As to the Conchostracans with radial markings the number of genera went up to 9 in the period, but if the number of

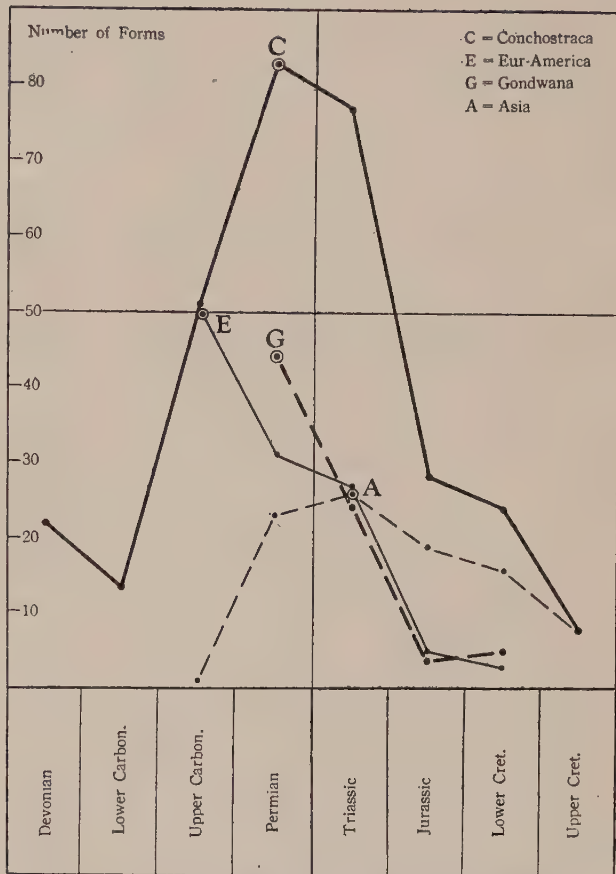


Figure 25. Rise and fall of the Conchostracans indicated by the number of forms.

species is taken, the late Carboniferous (30 forms) is superior to the Permian fauna (24 forms). Figure 25 clearly indicates the fact that the rise and fall of Conchostracans are reciprocal between Eur-America and Asia. The climax was in the late Carboniferous in the former but in the Triassic in the latter, the fact showing that the center of their distribution shifted from the former to the latter in the northern continents. In the latter they survived till the end of the Mesozoic era. During the shifting process Russia and Northern Siberia became the center of distribution in the late Permian and early Triassic periods. In the southern continents the Conchostraca developed sporadically in the Permian period, but later declined rather abruptly.

The rise of Conchostracans in Eastern Asia in the Mesozoic era is certainly a remarkable case of phyletic rejuvenescence. In this respect it is comparable to that of Stromatoporoids which also rejuvenated on the Pacific coast of Japan in the late Jurassic period. They were the leading rock builders of the Torinosu reef limestone a chain of which is traceable for a distance of 1000 km.

Not only in Estherians but there is also a great variety in Mesozoic naiads and other limnobios and geobios. As I discussed in some detail at the third congress of Carboniferous stratigraphy at Heerlen

(KOBAYASHI, 1951), the change from Palaeophyticum to Mesophyticum was gradual in Eastern Asia, because climatic and geographic changes were gradual there at the time of the Variscan cycle. The change was greater between the late Permian and early Mesozoic floras because the orogenic movement shifted from the west to the east and in the latter it attained its paroxysm in the middle Triassic period.

Because the rise and fall of land life are so intimately related to a cycle of orogeny, the shifting of the center of Conchostracan distribution endorses the view that the orogenic cycle shifted from the Variscan in Europe to the Akiyoshi in Eastern Asia as I claimed in my "Sakawa Cycle" (1941).

As the orogenic storm thus shifted, the center of Conchostracan distribution was compelled to shift to Russia, Central Siberia and Central Asia in the Permo-Triassic period. As pointed out already, paroxysm of deformation in the Kuznetsk basin must be in middle Triassic, if not late Triassic. The strong crustal deformation at the time can be expected to have been strong also in Central Asia, (see page 101). There is some evidence promising fruitful results for Estherian hunting in Central Asia.

Two kinds of Estherian fauna are distinguished in Eastern Asia. One is the synorogenic fauna in the pericontinental zone and the other the interorogenic fauna in the intracontinental terrain. The two kinds of Estherian groups can be combined in a suite. Akiyoshi and Sakawa suites thus figured out are two biocycles which correspond respectively to the orogenic cycles of Akiyoshi and Sakawa. The two kinds of the Estherian fauna are typically represented in certain faunas in the southern continents. The Upper Triassic fauna of the Congo-Angola basin is an example of the kratonic type of fauna in the interior of the continent in which polymorphic *Euestheria angolensis* occurs. The late Permian fauna of New South Wales which reveals strong morphic diversity is a typical example of the orogenic type.

Insofar as adaptative radiance is concerned, *land life depends more on orogeny than on epirogeny as marine life does more on epirogeny than on orogeny.* This is because the expansion of the habitat and a great variety of environments are brought about by crustal movements. The negative epirogeny causes the sea to flood over the continental shelf and rich marine faunas are found in the belt of variables. The influence of orogeny on land life is not essentially

different from it. Polymorphism is high in large basins embraced by arcuate mountains. The variation and isolation of the habitats in mountains and intermontane basins are two of the important factors which cause morphic diversity, although there may be other reasons in the bios themselves.

3. Phylogenetical relationship among the non-marine Conchostracan genera and families

Aside from a doubtful *Palaeolimnadiopsis eifelensis* the Devonian Estherians are represented by many *Asmussia* with subcentral umbo on the straight dorsal margin as well as by *Cyclestherioides*, *Euestheria* and *Lioestheria*, the last two of which have subterminal umbones on subovate carapaces. The test is punctate in *Lioestheria*, but reticulate, radially lined, or smooth in *Euestheria*. These two are comprehensive and persistent genera which survived until the Cretaceous period. *Asmussia* and *Cyclestherioides* are also long-ranged.

An important question is which is more primitive—the Conchostracan with the subcentral or the subterminal umbo? *Euestheria malangensis* might show the change from the former to the latter through growth, although there are still some questions on the morphic series illustrated by MARLIÈRE. (See page 46). Nevertheless it is noteworthy that the Conchostracans with subcentral umbones are well represented in the Devonian period when *Asmussia* was at the height of its development. They are probably related to *Rhabdostichus*.

There was not much change in the early Carboniferous in generic assemblage, but in the late Carboniferous period *Estherites* was added to the Lioestheriinae, and the Limnadiidae also appeared. Which one of the pre-existing genera is ancestral to *Estherites*, is an open question. At any rate they persisted till the Cretaceous period.

The number of claspers provides generic distinction for *Limnestheria*, but distinction is based on carapace for all other genera. In *Cornia* the center of the incipient carapace lies at a point below the dorsal margin and a smooth tubercle-like elevation in the umbonal area suggests a swelling of the body during rapid growth in immature stage. It is probable also that the swell served in the attachment of the body to the carapace. The projection of the posterior margin along the dorsal one in *Palaeolimnadiopsis* may have been for protection of the rear part. Otherwise its carapace is similar to *Euestheria*

and *Lioestheria*. Because they are all inhabitants in the *Kohlengürtel*, it is quite reasonable to consider that morphic diversity of the carapace is due to variation and isolation of the coal basins in the *Gürtel*. Neither of them, however, indicates high specialization.

Palaeolimnadiopsis is not a large but long-ranged genus which occurs discontinuously until the end of the Cretaceous period. Tatarian *Vertexia* also has posterior sinuation, but its posterior end forms a series of spines through growth. In addition, there is a large spine issuing dorso-laterally from the umbonal swell. Therefore it is certain that it was derived either from *Palaeolimnadiopsis* or from *Cornia*.

In the late Permian period there appeared archaeic forms of *Estheriina* in which the umbonal swell is much larger than in *Cornia* and the peripheral flat band very narrow when compared with those of the Bahian forms of *Estheriina*. Whether these Permian ones are related to *Cornia* or Bahian *Estheriina* cannot be told. Seeing that similar forms occur in Japan, North Siberia, Africa and North America in the Triassic formations, it is probable that the swelling of the carapace appeared intermittently without any phylogenetical relation.

Echinestheria in the Upper Triassic of the Congo basin has an umbonal spine but there may be no direct relation with *Vertexia*.

From a morphological standpoint it can be said that the genera provisionally referred to the Limnadiidae reveal one or other common characteristics which suggest grouping them into a family or subfamily. Some of them which are short-ranged are highly specialized. The others occur in two or more periods, but their occurrences are isolated geologically as well as geographically, the status casting doubt on their genetical relationship.

Most of the Lioestheriidae are persistent form-genera mostly ill-defined, but *Pseudoleaia* in the Cretaceous of Japan is an exception which appeared in phyletic senility by high specialization, probably from *Euestheria*.

The Estheriellidae comprise parallel off-shoots from Lioestheriidae or the Limnadiidae in the similar evolutional trend. The oldest of the family is *Praeleaia* in which 4 or 5 radial ribs are well developed. In Upper Carboniferous *Anomalonema* the radial markings are much weaker and more numerous than those of *Praeleaia*. It is probable that these fine ribs were introduced by the development of radial lirae. In *A. reumouxi* the posterior margin is sinuated like in *Palaeo-*

limnadiopsis. It is, however, an open question whether the sinuation indicates the derivation of *Anomalonema* from the Limnadiidae stock, or whether it appeared in *Anomalonema* independent from the family but parallel to the evolutional trend of that family.

There is no link between Upper Carboniferous *Anomalonema* and Triassic *Estheriella*. Several ribs are usually strengthened in the medio-ventral part of the carapace in *Estheriella*. It is very doubtful that *Estheriella* of the Buntsandstein is actually related to the so-called *Estheriella* in the Permo-Triassic of Africa. *Nyasestheriella* and *Congestheriella* are established for *Estheriella nyasana* and *Estheriella lualabensis* respectively, because they are so different from *Estheriella* s. str. in outline and mode of ornamentation. *Estheriella bornhardti* is also fairly distinct from *Estheriella* and possibly represents a new genus. *Estheriella moutai* is the nearest to *Estheriella*, but its radial ribs are much stronger and do not become slender on the lateral sides as in *Estheriella*. Their common occurrences in varicoloured sediments suggest that dry inland basins were suitable for Estheriellians.

Metaleaia triassiana from the lower Triassic of Kuznetsk basin represents an independent genus from all others of the Estheriellidae. The definite number of nodose radial ribs of the same strength, regularly disposed with uniform intervals indicate higher specialization than *Estheriella*.

The presence or absence of radial marking in the umbonal area must be heavily evaluated in the classification, because it is known in living Estherians that carapaces with growth lines are not cast off at the time of moulting. Therefore the umbonal area devoid of radials indicates the Estherian stage in the carapace growth of the Estheriellidae which came after the nauplius stage. The development of radials on the carapace is gradual in this family but quite abrupt in the Leaiadidae. They appear sporadically after the nauplius stage.

In view of the usual absence of the radial markings in the umbonal region, all of these Estheriellians, even *Metaleaia*, are not related to the Leaiadidae. Some of them are considered to have been derived from the Lioestheriidae, but it is probable that a part of them are derivatives from the Limnadiidae. Thus the family is a polyphyletic aggregate.

RAYMOND considered the Leaiadidae to be polyphyletic, but I think it to be monophyletic because the above mentioned characteristic

can be recognized in all the Leaians. Its ancestor is unknown, but from *Eoleaia* it is presumed to have had a relatively long subquadrate carapace and a terminal umbo. After the Acadian disturbance the family appeared in Nova Scotia. *Eoleaia* with two radial ribs is the most primitive genus from which *Leaia* developed by strengthening these ribs in addition to the hinge margin. Thus the carinae and also the nodes came into being to strengthen the carapace. The hollow carinae and the concavity in their intervals suggest complicacy of the internal structure. As a great variety of *Leaia* is seen in coal-bearing formations, *Leaia* may have preferred humid climate. As in the Lioestheriidae, there occurred at first a great variation in carapace outline. LASPEYRES (1870) distinguished subrectangular and suboval forms. The two groups correspond to RAYMOND's *Leaia* and *Hemicycloleaia*. Seeing various species of Leains, however, their distinction is found artificial, because there is no sharp boundary. It is my opinion that it is better to eliminate aberrant forms from *Leaia* as it is too comprehensive.

Paraleaia, *Bileaia*, *Trileaia*, *Quadrileaia*, *Discoleaia*, *Monoleiolophus* and *Acantholeaia* are all clear-cut genera, although they are all represented by one or a few local species. They as a whole indicate wide divergence in the phylogerontic stage in the late Permian. *Monoleiolophus* is a single exception which had appeared already in the Pennsylvanian. *Monoleiolophus* comprises a few other Upper Permian species from Russia, Brazil and (?) Australia. Their distribution does not help much in considering their genetical relation, but *Monoleiolophus* evidently comprises forms developed in the same degenerating trend. The disappearance of the anterior carina is a trend of evolution, as indicated by Pennsylvanian *Leaia acutangularis* and Stephanian *Leaia wettinensis*.

As indicated by the increase of angle α in the Carboniferous species of *Leaia* in Europe, the disposition of carinae on the carapace is changeable. While the position of the existing carinae shifted, new carinae were added in the interspaces. *Bileaia*, *Trileaia* and *Quadrileaia* all are genera which appeared at length in the late Permian along such evolutional trends. *Discoleaia*, however, is different. It represents a terminal in the modification of the carapace outline.

The appearance of radial ribs in *Eoleaia* is sporadical, but various Leaians show a change of radial markings from simple ribs to nodose carinae through carinae without nodes. Later the carinae tended to

die out near the periphery in some, and in some others intervals of the anterior carina became obsolete and only the nodes remained before the carina disappeared completely. Beside such reduction of the carina there occurred the lateral shifting of the carina and the addition of a fold, furrow or carina. Such an additional radial marking starts from the umbo, but generally dies out before reaching the periphery.

Acantholeaia is the most peculiar Leaian having three carinae with spines on the subdorsal carina. Spines exist in *Vertexia*, *Acantholeaia* and *Echinestheria*, all in variegate sediments in which coal measures are undeveloped, though the position and prominence of the spines are not the same among these genera. The appearance of the spines in the Conchostraca presumably has something to do with the physical condition of their habitats in the arid inland basin. The spiny armours of *Acantholeaia* as well as *Vertexia* may be an indication of severe struggle for existence in the late Permian.

At the end of the period the Leaiadidae were conquered by their enemy almost completely, leaving *Mesoleaia nodosocostata* in the Buntsandstein which is a possible relict of the family. Because it is an evolutional trend for carinae to increase, it is quite reasonable to expect a quinquicarinate genus in the end.

There are more species of the Leaiadidae in the Upper Carboniferous than in the Permian, but if the number of genera is counted, the latter period is incomparably superior to the former. This difference implies a difference in morphic radiance within a genus or within a family. While Estheriellians are thought from their habitats to have been mostly arid climate lovers, the great development of *Leaia* in the *Kohlengürtel* strongly suggests that *Leaia* was a humid climate thriver. This may be one reason for the wide radiance of the Leaiadidae in arid Permian inland basins.

4. The evolution of the Conchostraca

Péneau described *Estheria buchoti* from the schistes à *Ceratiocaris* at Moulin de Régereau in France, which is considered to be probably Upper Gotlandian (or Devonian), because the shales lie on the Middle Gotlandian nodules calcaires à *Orthoceras* and *Cardiola interrupta*. It belongs to Raymond's *Rhabdostichus* of which Clarke's *Estheria pulex* from the Middle Devonian Hamilton in New York is the type. There

it is associated with ostracodes and a *Discina*. They were probably near-shore inhabitants. CLARKE's has narrow striae and PÉNEAU's very fine reticulae in the interspace. The subcentral beaks of the two species and the straight dorsal margin of the latter agree with those of *Asmussia*, although *Asmussia* has no concentric undulations as seen in *Rhabdostichus*. Its being a Conchostracan genus is highly probable, but at the same time the concentric undulations are such a distinct characteristic that they are never seen in the non-marine Conchostraca, if the dubious "*Estheria*" *minoprioi* is excluded. Therefore RUSCONI's proposal of the Rhabdostichidae is of value. I cannot, however, convince myself of the appearance of *Rhabdostrichus* (? *cuyanensis*) in the Middle Cambrian.

Schizodiscus has two semi-circular valves fused along the dorsal margin. It is represented by *Schizodiscus casper* CLARKE and *S. antecrenulus* CLEAVES respectively from the Hamilton formation in New York and Pennsylvania. The umbo is small, smooth and elevated at the beak and some 30 sharp concentric ridges are crenulated by transverse ridges in the anterior part of the latter.

As no Estherian sculpture is recognized in the interspaces and the valves are usually wide open, the Lioestheriidae are more remote from *Schizodiscus* than *Rhabdostichus*. The carapace of *Schizodiscus* suggests its alliance to Peltocarids. ULRICH and BASSLER (1931), however, noted the remarkable resemblance of the genus to *Lepiditta* MATTHEW, 1886, notwithstanding the fact that the two valves are thought to have been closed in *Lepiditta*, their outline being much narrower and subacuminate and the concentric markings of the regular carapace less regular and not ridge-like. Judging from the preponderance of marine elements in the Hamilton fauna, *Schizodiscus* is a marine, rather than a non-marine inhabitant occurring as a wash in the Hamilton sediment.

The available evidence is not enough to decipher the story of Conchostracan evolution, but it is quite probable that Estherians were derived from some marine ancestor like *Rhabdostichus* near the closing of the Gotlandian period, probably by the locking of the ancestor in a lagoon or a lake which was cut-off from the sea by crustal deformation in the *Ardennisch* or *Erisch Phase* of the Caledonian cycle.

Like Estherians of that time, *Trigonioides* (KOBAYASHI and SUZUKI, 1936) was derived from the marine Trigoniidae as a relic in the early Cretaceous Wakino lake in northern Kyushu which came out after

the emergence of the previous embayment by the Oga orogenic movement. The Permo-Carboniferous naiads appeared in the Variscan cycle probably in some similar way. The relic fauna of the Caspian sea is a present day example. In the case of non-marine Molluscans such a change of habitat occurred more than once. But it is not neccessary for the Conchostraca to have such an event happen more than once because their wide dispersal is attributable to the transportation of their egg-capsules by wind.

It is certain that Middle Devonian *Asmussia murchisoniana* in Scotland and its adjacence adapted itself to the enviroment of lake Orcadie. But it may not be simply a dream to think that older Estherians could live in brackish near-shore, as suggested by CHERNYSCHEV.

In agreement with RAYMOND (1935), I think the Bradorina which comprise the Bradoriidae MATTHEW, the Beyrichoidae ULRICH and BASSLER and the Indianidae ULRICH and BASSLER are quite distinct from the Conchostraca, because they have no growth lines and many of them have the so-called ocular spot or muscular scar located high in the anterior part. The ventral ridge and the peripheral narrow band in some species show that they are certainly more closely allied to the Ostracoda than to the Conchostraca, although their test is less calcareous.

On the contrary, a few Cambrian species which ULRICH and BASSLER referred to the Limnadiidae in their monograph appear to be ancestral to non-marine Conchostracans. Therefore I propose the Lepidittidae to include *Lepiditta, Modioloides* and *Fordilla* (?). Although I have not examined them myself, their tests are calcarophosphatic according to ULRICH and BASSLER and apparently lack the Estherian type of sculpture. In outline *Lepiditta alata, Modioloides prisca* and *Fordilla troyensis* are respectively similar to *Asmussia, Estherites*, and *Euestheria*. The last species has many fine concentric lines similar to those in *Euestheria*. It is, however, an open question whether *Fordilla* is a pelecypod or a Conchostracan. The distribution of the family is, however, restricted to the Cambrian marine sediments on the Atlantic side and there is unfortunately a large break in the record from Ordovician to Gotlandian.

Another puzzle is why there is no Tertiary Estherian fossil. PACKARD's *Estheria dawsoni* (1881) from the post-glacial Mallotus beds, east of Ottawa, Canada, is probably a teleostean fish-scale, according to

Table X. Geological range of the Conchostracan genera.

Fossil Conchostraca	Geological Age	Cambrian	Ordovician	Gotlandian	Devonian	Carbon. Lower	Carbon. Upper	Permian	Triassic	Jurassic	Cretaceous
Lepidittidae	*Lepiditta*	×									
	Modioloides	×									
	(*Fordilla*)	×									
Rhabdostichidae	*Rhabdostichus*			(×)	×						
Lioestheriidae	*Euestheria*				×	×	×	×	×	×	×
	Lioestheria				×	×	×	×	×	×	×
	Asmussia				×	×				×	×
	Quadriasmussia					×					
	Estherites							×	×	×	×
	Cyclestherioides				×		×	×	×	×	×
Limnadiidae	*Estheriina*						×	×	×		×
	Cornia						×	×		(×)	
	Echinestheria								×		
	Palaeolimnadiopsis					×	×	×			×
	Vertexia							×			
Lynceidae	*Lynceus*										×
	Limnestheria						×				
Estheriellidae	*Praeleaia*				×						
	Anomalonema						×				
	Nyasestheriella						?				
	Congestheriella							×			
	Estheriella								×		
	Metaleaia								×		
Leaiadidae	*Eoleaia*					×					
	Leaia					×	×	×			
	Monoleiolophus						×	×			
	Discoleaia							×			
	Paraleaia						×	×			
	Bileaia							×			
	Quadrileaia							×			
	Trileaia							×			
	Mesoleaia								×		
	Acantholeaia							×			
Total		3		(1)	6	7	11	17	10	4.5	8

RAYMOND. No clue to the solution of this problem has been found, but it is not improbable that the Conchostraca developed again abruptly in pools in the inter- and post-glacial periods.

Whatever the answer may be, discontinuous distribution between

the fossil and living Conchostraca may be compared with that between the Heliolitidae and the Helioporidae, the former family ranging from Ordovician to Devonian and the latter from Cretaceous to Recent. In each of these two pairs of discontinuous groups the exoskeletons look a like. Thoughdisconnected, Cretaceous and older Estherians are evidently ancestral to the living ones. The Lynceidae had already existed in the early Cretaceous and possibly in the late Carboniferous period, as documented by *Limnestheria ardra* and a few others which retain some appendages.

CHAPTER VI

The classification of the fossil Conchostraca

1. New species and new names

Starting from artificial taxonomy, I tried to institute a natural classification for the fossil Conchostraca. It was considered from various angles with the result some information was brought to light on the history of their development, but we are still far from knowing the genetical relationship among the various groups of the Conchostraca and their ally, especially the Estherians. The scheme of classification proposed here is tentative and some genera and families are simply morphic groups.

In the course of this study I have found several new forms and preoccupied names for which I have taken the liberty of denomination. They are listed below.

1. *Euestheria kidoi* KOBAYASHI, sp. nov. i.e. *Estherites* aff. *reticulatus* by KOBAYASHI, (non CHERNYSHEV), 1951, pl. I, fig. 9. See page 63.
2. *Euestheria kusumii* KOBAYASHI, sp. nov. i.e. *Estherites* aff. *transbikalica* by KOBAYASHI, (non CHERNYSHEV), 1951, pl. I. fig. 4. See page 63.
3. *Euestheria mansuyi* KOBAYASHI, sp. nov. i.e. *Estheria minuta* by MANSUY, (non VON ZIETEN), 1912, pl. 10. fig. 3a. See page 47.
4. *Lioestheria lutkevichi* KOBAYASHI, sp. nov. i.e. *Estheria exigua* by LUTKEVICH, (non NETSCHAJEW), 1941, pl. 1, fig. 6. See page 99.
5. *Lioestheria pseudominuta* KOBAYASHI, sp. nov. i.e. *Estheria minuta* by LUTKEVICH, (non VON ZIETEN), 1927, text-fig. p. See page 41.
6. *Cyclestherioides grossi* KOBAYASHI, nom nov. i.e. *Cyclestherioides subcircularis* (RAYMOND), 1946, non CHERNYSHEV, 1934. See page 87.
7. *Cyclestherioides janenschi* KOBAYASHI, sp. nov. i.e. *Estheria tendagurensis* JANENSCH (text-fig. 2), 1933, fig. 2. See page 22.
8. *Cyclestherioides picardi* KOBAYASHI, sp. nov., i.e. *Estheria minuta* by PICARD, (non VON ZIETEN), 1911, pl. 23, fig. 2. See page 98.
9. *Cornia* (?) *novozhilovi* KOBAYASHI, nom. nov., i.e. *Cornia* (?) *limbata* NOVOZHILOV, 1946, (non GOLDENBERG ,1877).
10. *Leaia raymondi* KOBAYASHI, nom. nov. i.e. *Leaia pruvosti* RAY-

MOND, 1946, (non REED, 1929). See pege 93.
11. *Monoleiolophus conemaughensis* KOBAYASHI, nom. nov. i.e. *Monoleiolophus unicostatus* RAYMOND, 1946, (non REED). See page 90.
12. *Trileaia sulcata* KOBAYASHI, sp. nov., i.e. *Leaia* sp. indt. MITCHELL, 1925, pl. 43, fig. 20. See page 108.
13. *Paraleaia fritschi* KOBAYASHI, sp. nov., i.e. *Leaia wettiensis* by FRITSCH, (non LASPEYRES) in BEYSCHLAG and FRITSCH, 1900, pl. I, fig. 4. See page 94.
14. *Trileaia etheridgei* KOBAYASHI, sp. nov., i.e. *Leaia* sp. indt. MITCHELL, 1925, pl. 43, fig. 21. See page 109.

2. The scheme of classification

The classification of the fossil Conchostraca into genera is made here chiefly on the basis of discontinuity in morphic series or distinguishing aspects of the carapace, without regard to the number of species in a genus. Therefore many Estherian genera are synonymised, but aberrant forms are segregated as distinct genera. Such forms were found more among Leaians and Estheriellians than among Estherians.

The Cyzicidae and the Leptestheriidae are almost impossible to distinguish one from the other on the basis of the carapace alone. *Cyclestheria hoslopi* is distinct from them. Many fossils which are collectively called *Cyclestherioides* show different degrees of similarity to it and the boundary of this genus from the other Estherian genera is not very sharp. Therefore I was forced to erect the Cyclestherioidinae in the Lioestheriidae. In consequence the Cyclestheriidae with the other two families in Neontology are combined into the Lioestheriidae in Palaeontology.

There is no living Conchostracan with radial markings, but there were various forms of such Conchostracans in the past. The Estheriellian genera are probably polyphyletic, but grouped in the Estheriellidae because their radials are usually finer and more numerous than in the Leaiadidae and have become obsolete near the umbo. This family is a closer relative of the Lioestheriidae than the Leaiadidae and thought to have branched off from the Lioestheriidae or in part from the Limnadiidae from time to time in different regions with similar trends.

The Leaiadidae are presumed to have been derived from the Lioes-

theriidae some time in the transition from the Devonian to the Carboniferous period. Since the late Carboniferous period this family has developed with various trends, but it is monophyletic, although similar forms of isolate occurrences are grouped together in certain genera.

In adding archaeic marine Conchostracans to non-marine ones over 320 fossil forms are classified here in 33 genera in 7 families where *Bileaia*, *Congestheriella*, *Discoleaia*, *Eoleaia*, *Mesoleaia*, *Nyasestheriella*, *Quadriasmussia*, *Quadrileaia* and *Trileaia* are new.

Phylum Arthropoda, Class Crustacea, Subclass Branchiopoda.
Order Conchostraca.

Diagnosis:—Carapace chitinous, little calcified, or rarely corinous, bivalved by folding along the dorsal margin and marked by concentric lines, ridges or undulations except the Lynceidae. Outline of the carapace semicircular, subcircular, subelliptical, subovate subtriangular or subquadrate subtrapezoidal, or may be subangulate at the posterior end of the dorsal margin or at the end of the radial carina. Posterior margin sometimes slightly alate near the dorsal margin, but no deep or large sinuation. No ocular spot or muscular scar known on fossil carapace. Their interspace smooth or marked by Estherian sculpture which consists of minute punctae, polygons, reticulae or radial lirae, branching or unbranching. Umbo located somewhere between the median point and the anterior end of the dorsal margin, frequently a little projected above the margin but sometimes the center of the umbonal area is located a little below the dorsal margin. This area is sometimes smooth or swollen out, and rarely protruded into a spine. A few series of spines are met with in a few species along the dorsal margin. The Leaiadidae and Estheriellidae have various radial ornaments, —ribs, carinae, folds or grooves which are sometimes nodose. A series of spines exist in *Acantholeaia* on the subdorsal carina.

Distribution:—Gotlandian (?), Devonian to Cretaceous, Recent, with acmic prominence in Permo-Triassic period, nearly all non-marine, but Cambrian Lepidittidae all occur in marine sediments.

Family Lepidittidae KOBAYASHI, 1953

Diagnosis:—Carapace bivalved, similar to Estherians and mostly calcaro-phosphatic, but the Estherian type of sculpture unknown on the test.

More and better material is needed before the reference of this family to the Conchostraca can be made final.

Distribution:—Cambrian marine formations on the Atlantic side.

Genus *Lepiditta* MATTHEW, 1886

Diagnosis:—Carapace small, about 1 to 2 mm. long, obliquely semi-circular or semi-elliptical, higher in the anterior; umbo subcentral and low on the dorsal margin which is straight and long; test thin; surface marked with concentric lines or undulations and sometimes with fine radial lirae.

Type:—Lepiditta alata MATTHEW.

Remark:—In the outline of the carapace and the position of the umbo the type species is similar to *Asmussia*. Its test is said however to be probably calcareous. This as well as *L. curta* has subvertical anterior margins, but not *Bathocypris polita* STEUSLOFF (1894) which is referred to this genus by ULRICH and BASSLER (1931) with some doubt. In the last-mentioned a pair of linear grooves is widely divergent from the subcentral point of the dorsal margin.

Distribution:—Lower (?) and Middle Cambrian of New Brunswick and Upper Cambrian glacial boulder in Germany; *polita* is found in association with *Parabolina*.

Genus *Modioloides* WALCOTT, 1889

Represented by a right (?) valve of *Modiolopsis* (?) *prisca* WALCOTT from the Lower Cambrian of New York, which is roundly subquadrate and fairly convex; umbo subcentral; test calcaro-phosphatic. The type valve is about 2 mm. high, slightly less than 3 mm. long. WALCOTT (1890) illustrated a clear-cut elevation like an anterior adductor scar which, however, cannot be seen in ULRICH and BASSLER's photograph of the type specimen. According to ULRICH and BASSLER (1931) the scar is an accidental product of secondary deformation.

? Genus *Fordilla* BARRANDE, 1881

Minute modioloid valves with umbones between the center and the anterior extremity of the valves; a lunule-like sinuation found in front of the umbo; growth lines fine and dense; internally, wrinkles radiating postero-ventrally from the umbo; test calcaro-phosphatic (?); valve scarcely higher than 4 mm. and longer than 6 mm.

The type specimen of *Fordilla troyensis* BARRANDE was collected from the Lower Cambrian at Troy in New York.

SHALER and FOERSTE's specimens from the Lower Cambrian of North Attlebourgh, Massachusetts (1888) is an internal mould having a subelliptical outline, more strongly convex on the dorsal than on the ventral side. There is a strong sinuation behind the front. The authors hesitate to identify it with *troyensis*. According to GRABAU (1900) it is probably *Watsonella crosbyi*. DELGADO's specimens of *troyensis* (?) from Alemtjo, Portugal (1904), are badly deformed.

In the Hartshill specimen of COBBOLD's *troyensis* the lunule-like depression is absent and the dorsal half is obtusely triangular. In POULSEN's specimen of *troyensis* in fig. 5, pl. 2, an umbo appears to be swollen out. There growth lines are discernible but weaker than in the other part. In the other specimen in fig. 3 which is much taller there are two kinds of concentric lines, some of them being more strongly impressed than the others in the interspace between the strong ones.

In agreement with WALCOTT (1886), POULSEN (1932) regards *Fordilla troyensis* as a pelecypod because the thickness of the shell in his collection exceeds that of the Cambrian Crustacea except the trilobites. In his specimens from the Lower Cambrian Bastin formation of East Greenland, the shell presumed to have been of aragonite, is replaced by calcite. There is however no pelecypod in the Middle and Upper Cambrian faunas.

Family Rhabdostichidae RUSCONI, 1946
Genus *Rhabdostichus* RAYMOND, 1946

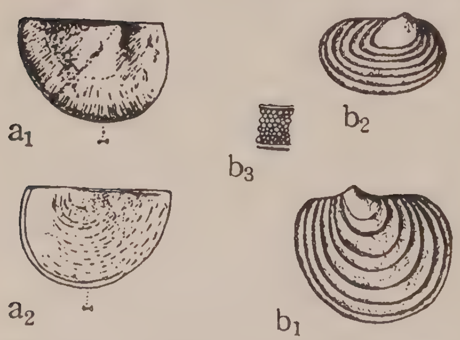


Figure 26. *Lepiditta* and *Rhabdostichus*.
a_{1-2}. *Lepiditta alata* (MATTHEW)
b_{1-3}. *Rhabdostichus buchoti* (PENEAU)

Diagnosis:—Conchostraca with concentric undulations and striated or reticulated test; beak subcentral.

Type:—*Estheria pulex* CLARKE.

Distribution:—Upper Gotlandian (or Devonian) of France and Middle Devonian of eastern North America, both in marine facies. Occurrence in the Middle Cambrian in South America is not certain.

Family Lioestheriidae RAYMOND, 1946

Diagnosis:—Conchostraca with growth lines on the carapace; test smooth or ornamented with Estherian type of sculpture.

Distribution—Devonian to Cretaceous.

Subfamily Lioestheriinae KOBAYASHI, new subfamily

Diagnosis:—Lioestheriidae with subovate or subelliptical carapace, longer than high, and terminal or subterminal umbo.

Distribution:—Devonian to Cretaceous.

Genus *Euestheria* DEPÉRET and MAZERAN, 1912

Synonyma:—Bairdestheria RAYMOND, fossils, *Polygrapta* NOVOZHILOV, *Howellites* BOCK, *Estheriellites* BOCK.

Diagnosis:—Lioestheriinae with smooth interspace, or ornamented by radial lirae or reticulae or both.

Type:— Posidonia minuta VON ZIETEN.

Distribution:—Lower Devonian to Upper Cretaceous. The genus is ill-defined and hence comprehensive. Among some 100 forms referred to it, three quarters are distributed in the northern continents. In the Permian and three Mesozoic periods there were 20 species or so in each; about 10 in the Carboniferous and 3 or more in the Devonian period.

Genus *Lioestheria* DEPÉRET and MAZERAN, 1912

Synonyma:—Palaeestheria BERNARD, *Pseudestheria* RAYMOND, *Diaplex* NOVOZHILOV, *Diaphora* NOVOZHILOV.

Diagnosis:—Similar to *Euestheria*, but the sculpture dominantly punctae or granulae.

Type:—Estheria lallyensis DEPÉRET and MAZERAN.

Distribution:—Lower Devonian to Lower Cretaceous. *Lioestheria* comprises 35 to 40 species some six-sevenths of which are known from the northern continents. The genus was most developed in the Permo-Triassic when more than 25 species lived.

Genus *Pseudoleaia* KOBAYASHI, 1953

Diagnosis:—Lioestheriinae with subquadrate carapace and one or two very weak diagonal elevations; vertical straight anterior margin forms a right angle with the slightly arcuate dorsal margin; carapace fairly convex.

Type:—Estheria rectangula YOKOYAMA, monotypic.
Distribution:—Neocomian of Japan.

Subfamily Asmussiinae KOBAYASHI, new subfamily

Diagnosis:—Lioestheriidae with subcentral umbo on the valve; test smooth, punctate, reticulate or lined radially.

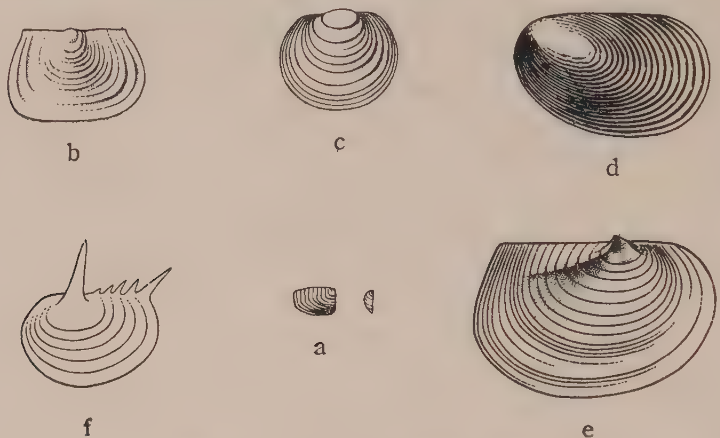


Figure 27. Some Estherian genera.

a. *Pseudoleaia rectangula* (YOKOYAMA)
b. *Quadriasmussia hercynica* (KUMMEROW)
c. *Cyclestherioides picardi* (KOBAYASHI)
d. *Cornia papillaria* (LUTKEVICH)
e. *Echinestheria marimbensis* (MARLIÈRE)
f. *Vertexia tauricornis* (LUTKEVICH)

Remarks:—Asmussia sporadically developed in the middle Devonian but gradually declined toward the early Carboniferous period when *Quadriasmussia* appeared as its off-shoot. *Asmussia*, however, did not die out until the middle Cretaceous. *Estherites* which is thought to have sprung out probably from *Asmussia*, showed no significant development, but persisted till the end of the Cretaceous period.
Distribution:—Middle Devonian to Cretaceous.

Genus *Asmussia* PACHT, 1852

Synonym:—Erisopsis RAYMOND.
Diagnosis:—Asmussiinae with tall carapace; hinge margin straight or nearly so.
Type:—Asmussia menbranacea PACHT.
Distribution:—Middle Devonian to Middle Cretaceous, but most developed in the Devonian. This genus comprises some 15 species.

As shown by a statement of RAYMOND that this genus "appears to be a good Devonian index fossil", about two-thirds of the species are Devonian and a half of these are Middle Devonian. There are, however, two or three Lower Carboniferous species, two Rhaeto-Liassic and one Lower or Middle Cretaceous species. Most of them occur in Eurasia and a few in North America. None is known from the southern continents.

Genus *Quadriasmussia* KOBAYASHI, new genus

Diagnosis:—Similar to *Asmussia* but the outline of the carapace is subquadrate, expanded ventrally, instead of well rounded as in *Asmussia* except at the dorsal margin. The umbo is a little projected above the straight dorsal margin.

Type:—Estheria hercynica KUMMEROW, monotypic.

Remark:—The small swelling umbonal area provided with two or three concentric ridges and grooves is located a little anterior to the median point of the dorsal margin which is slightly shorter than the length of the carapace. The valve is nearly equilateral but the posterior margin is more strongly arcuate than the anterior and apparently curves back a little near the dorsal margin. The concentric markings are round-topped ridges separated by relatively narrow grooves. The sculpture is unpreserved on the holotype but the *Gitterskruptur* is found in others at the same locality. This genus is clearly distinguished from all other Conchostracan genera by the combination of these characteristics. The holotype is 33.5 mm. high and 4 mm. long.

Distribution:—Lower Carboniferous (Kulm) of Harz, Germany.

Genus *Estherites* KOBAYASHI and HUZITA, 1941

Synonyma:—Palaeolimnadia RAYMOND, *Orthothemos* RAYMOND.

Diagnosis:—Asmussiinae with subelliptical or subquadrate carapace, much broader than *Asmussia*; dorsal margin more or less arcuate.

Type:—Estheria mitsuishii KOBAYASHI and HUZITA.

Remark:—The application of this generic name is restricted to forms as defined above.

Distribution:—Lower Permian to Upper Cretaceous. Among some 15 species two-thirds are distributed through these systems in Eurasia. More precisely, Permian ones in Russia and Rhaetic and later ones in Eastern Asia are linked by an Anisic species from the Anabar basin

in northern Siberia. There is an European Jurassic species. In addition, 4 late Permain species and 2 late Triassic species are known from Africa and Brazil.

Subfamily Cyclestherioidinae KOBAYASHI, new subfamily

Diagnosis:—Lioestheriidae with subcircular carapace, or at least the medio-ventral outline semicircular.

Remarks:—This subfamily is represented only by *Cyclestherioides*. Morphologically, it seems to be closely related to *Asmussia*, but which of the two is ancestral to the other is an open question. A species of *Cyclestherioides* appears earlier than *Asmussia*, but there is a long break before the late Carboniferous period, while *Asmussia* is well represented by a series of species in this interval.

Genus *Cyclestherioides* RAYMOND, 1946

Type—Estheria lenticularis MITCHELL.

Remarks:—Generic concept is emended as mentioned above.

Distribution:—Lower Devonian to Middle Cretaceous. Some 15 species referred to the genus are known from various places and ages, two-thirds of which are in the northern continents and the rest in the southern continents; one-third of the species reported from the Palaeozoic and the remainder from the Mesozoic era. Eifelian *grossi* is the oldest, and none is known from the later Devonian or from the early Carboniferous.

Family Limnadiidae BURMEISTER, 1843

Diagnosis:—Conchostraca with prominent umbo or postero-dorsal projection.

Remarks:—Fossil genera are grouped into two new subfamilies because their relation to the living ones is not actually known.

Distribution:—Upper Carboniferous to Upper Cretaceous; Recent.

Subfamily Estheriininae KOBAYASHI, new subfamily

Diagnosis:—Limnadiidae with prominent umbo.

Distribution:—Upper Carboniferous to Lower Cretaceous.

Genus *Estheriina* JONES, 1897

Diagnosis:—Estheriininae with convex umbonal area and flattened peripheral band; growth lines distributed in the two parts.

Type:—Estheriina bresiliensis JONES.

Distribution:—From Upper Carboniferous to Lower Cretaceous. Several species occur intermittently at places widely apart from one another, namely in Upper Carboniferous of Europe, Upper Permian of Australia, Upper Triassic of Japan and Lower Cretaceous of Brazil. They may be polyphyletic, but are grouped in a genus simply on account of their morphic similarity.

Genus *Cornia* LUTKEVICH, 1938

Synonym:—*Pemphicyclus* RAYMOND.

Diagnosis:—Estheriininae with smooth tubercle-like umbonal elevation below the dorsal margin.

Type:—*Cornia papillaria* LUTKEVICH.

Distribution:—From Upper Carboniferous to Permian or Rhaeto-Liassic. If two species of provisional reference from the Andes and Africa are excluded, several species of the genus are all Permo-Carboniferous. One of them from Zambezi reveals the typical umbonal tubercle. All others were procured from Eurasia among which quite a variation can be seen in the outline of the carapace.

Genus *Echinestheria* MARLIÈRE, 1950

Diagnosis:—Similar to *Cornia*, but a spine issuing from the umbonal elevation.

Type:—*Estheria* (*Echinestheria*) *marimbensis* MARLIÈRE, monotypic.

Distribution:—Upper Triassic of Angola.

Subfamily Vertexiinae KOBAYASHI, new subfamily

Diagnosis:—Limnadiidae with growth lines curving backward near the dorsal margin.

Distribution:—Upper Carboniferous to Upper Cretaceous.

Genus *Palaeolimnadiopsis* RAYMOND, 1946

Synonym:—*Limnadopsis* HALL and SPENCER, fossils.

Diagnosis:—Vertexiinae with no umbonal spine.

Type:—*Palaeolimnadiopsis carpenteri* RAYMOND.

Remarks:—As pointed out on page 96, Conchostracan nature cannot be confirmed in the type species. RAYMOND'S *eifelensis* is probably a deformed *Lioestheria diensti*. A few limnadiformes are, however, found in the Permo-Carboniferous in Europe and Brazil and two in Eastern Asia. They are referred to this form-genus, although discontinuous distribution casts doubt on their genetical relation. In the

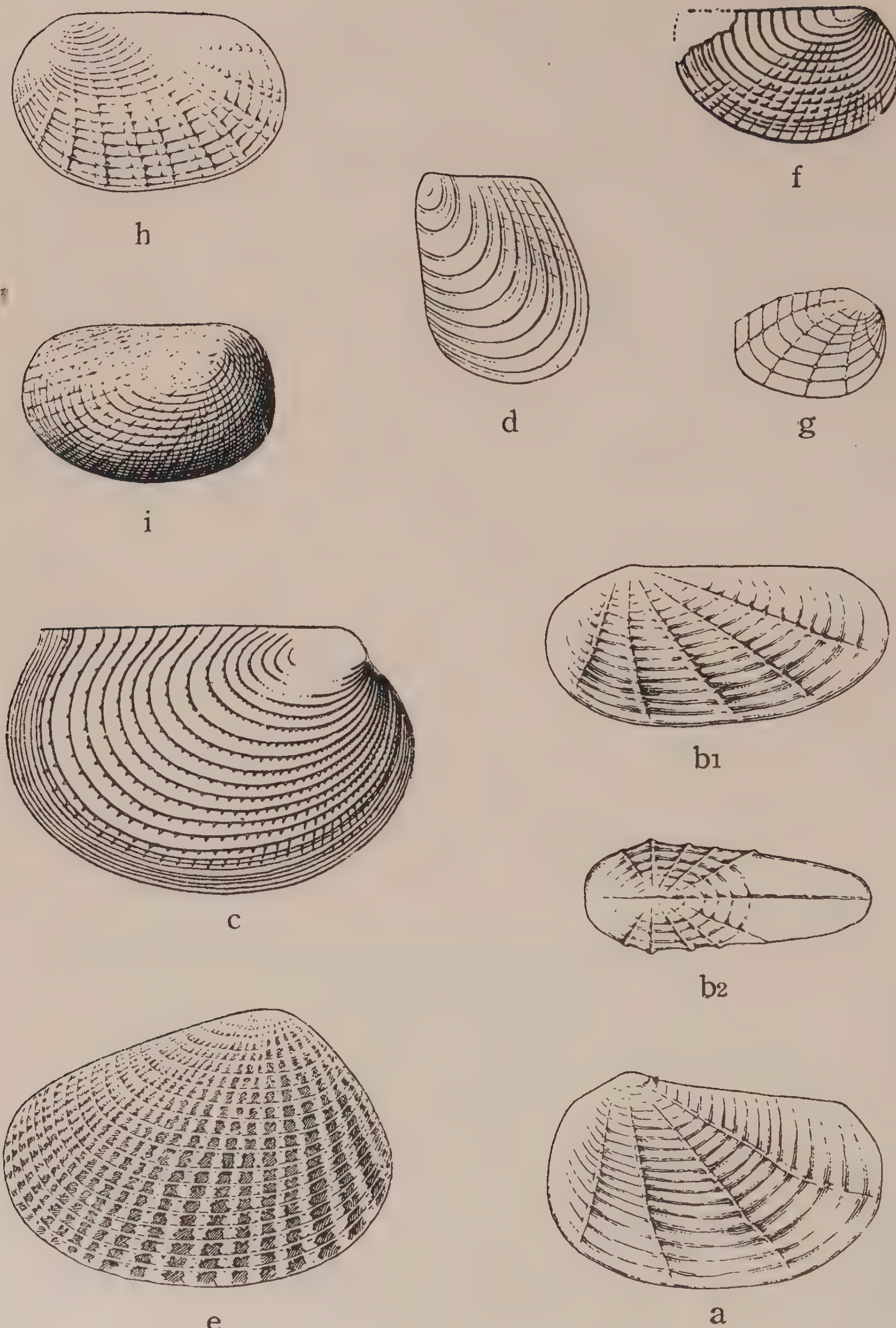

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illustration *Palaeolimnadiopsis sibericensis* appears to have some short spines along the dorsal margin.

Distribution:—Permo-Carboniferous and Cretaceous.

Genus *Vertexia* LUTKEVICH, 1941

Diagnosis:—Vertexiinae with a spine at umbo and a series of spines along the dorsal margin.

Type:—Vertexia tauricornis LUTKEVICH, monotypic.

Remarks:—The carapace is subovate in outline. While it is 2.5 mm. × 1.7 mm., the spine issuing from the relatively large juvenile carapace attains a length of 0.5 mm. and the posterior spine is 0.7 mm. long. The others on the dorsal margin are 0.3 mm. or less. Test is corneous; growth lines are 15 in number; interspace punctate.

Distribution:—Tatarian of Russia.

Family Lynceidae A. O. SAYCE, 1902
Genus *Lynceus* MÜLLER, fossils

Diagnosis:—Conchostraca with no growth line on the carapace.

Remarks:—Lynceus stchukini CHERNYSHEV, 1940, from the Lower Cretaceous of Transbaikalia is the solitary member in Palaeontology.

Genus *Limnestheria* WRIGHT, 1929

Diagnosis:—Lynceidae with only one pair of claspers.

Type:—Limnestheria ardra WRIGHT, monotypic.

Distribution:—Coal measures in Ireland.

Family Estheriellidae KOBAYASHI, 1953

Diagnosis:—Conchostraca with 5 or more radial ribs which become obsolete near the umbo.

Remarks:—This family is polyphyletic. Among the so-called *Es-*

Figure 28. Some Estheriellian genera.

a. *Praeleaia quadricarinata* (LUTKEVICH)
b. *Praeleaia quinquecarinata* (LUTKEVICH)
c. *Anomalonema reumouxi* PRUVOST (after RAYMOND)
d. *Nyasestheriella nyasana* (NEWTON)
e. *Congestheriella lualabensis* (LERICHE)
f. *Estheriella costata* WEISS (after SCHMIDT)
g. *Metaleaia triassiana* CHERNYSHEV (after CHERNYSHEV)
h. *"Estheriella" moutai* (LERICHE)
i. *"Estheriella" bornhardti* JANENSCH (after JANENSCH)

theriella from the Permo-Triassic of Africa. "*Estheriella*" *nyasana* NEWTON and "*Estheriella*" *lualabensis* LERICHE each respresents a new genus. "*Estheriella*" *bornhardti* JANENSCH may indicate still another genus. "*Estheriella*" *moutai* LERICHE from the Upper Triassic of Angola is the nearest to *Estheriella* s. str.

Distribution:—Middle Devonian to Upper Triassic; Europe, Siberia and Africa.

Genus *Praeleaia* LUTKEVICH, 1929

Diagnosis:—Estheriellinae with long and convex carapace and 4–5 ribs.

Type:—*Prealeaia quadricarinata* LUTKEVICH.

Remarks:—The anterior and posterior margins strongly rounded; ventral margin long and gently arcuate; umbo terminal and a little projected above the straight or nearly straight dorsal margin which is not carinate; 4 or 5 narrow ribs radiate from the dorsal end below the umbo and divide the valve into 5 or 6 sections of subequal breadth; anterior section lunate; concentric lines 15 to 18 in number, never geniculate, form a tubercle at each junction with the ribs.

Distribution:—Middle Devonian of Esthonia. The type species and *Praeleaia qninquecarinata* LUTKEVICH occur in the Pliusa river region.

Genus *Anomalonema* RAYMOND, 1946

Diagnosis:—Estheriellidae with many very fine radial ribs.

Type:—*Estheriella reumauxi* PRUVOST.

Remarks:—In the type species the outline of the carapace reveals a shallow postero-dorsal sinuation. Very fine riblets form small nodes in crossing growth lines. They become obscure near the umbo where, however, nodes can be seen. There are one Scottish and two Russian species of provisional reference.

Distribution:—Westphalian of Europe.

Genus *Nyasestheriella* KOBAYASHI, new genus

Diagnosis:—Carapace obliquely subquadrate, higher than long and fairly convex; umbo terminal on the nearly straight dorsal margin; ornamentation composed of some 20 equidistant concentric striation, fine lines in their interspaces and radial riblets, the last being distinct on the rear side; test thin, covered by fine pits and granules.

Type:—Estheriella nyasana NEWTON.

The monotype from the Permo-Carboniferous (?) or the Karroo formation of Nkana in Nyasa, is a very minute form, 1 mm. long, similar to certain naiads on cursory examination.

Genus *Congestheriella* KOBAYASHI, new genus

Diagnosis:—Carapace broadly ovate and strongly convex, provided with concentric lines and radial riblets regularly intercrossing, the former being continuous and the latter, cut by the former, nodose in the interspace.

Type:—Estheriella lualabensis LERICHE.

Remarks:—The monotype species from the Lualaba I (Upper Permian) of the Congo basin attains 3.7 mm. at its maximum length.

Genus *Estheriella* WEISS, 1875

Diagnosis:—Estheriellidae with several to some twenty or more radial ribs, which become weak on the anterior and posterior sides.

Type:—Estheriella costata WEISS, 1875, i.e. *Posidonomya wengensis* GIEBEL, 1857, non WISSMANN, 1841.

Remarks:—Besides the type species *Estheriella* comprises *E. weissi* and *E. lineata*. Their valves dilate toward the anterior third of their length where they are most high. The outline is subelliptical and radial ribs are strong in" *Estheriella*" *moutai*.

Distribution:—The genus s. str. is restricted to the Buntsandstein of Germany.

Genus *Metaleaia* KOBAYASHI, 1953

Diagnosis:—Estheriellidae with 5 radial ribs separated from one another by interspace of uniform breadth; intersections of several equidistant growth lines with the ribs and the dorsal margin nodose.

Remark:—Carapace is subovate cycladiform, tallest near the umbo; dorsal margin arcuate.

Type:—Estheria triassiana CHERNYSHEV, monotypic.

Distribution:—Lower Triassic of the Kuznetsk basin, central Siberia.

Family Leaiadidae RAYMOND, 1946

Diagnosis:—Conchostraca with radial ribs or carinae, 5 or less in number, which are divergent from the umbo, but not always reaching the margin; carinae sometimes nodose.

Remark:—The Estherian type of sculpture is seen in a few species of *Leaia* and *Monoleiolophus*. *Eoleaia* from the Chevirie formation in Nova Scotia is the most primitive of the family from which *Leaia* is thought to have been derived. *Leaia* comprising some 40 species forms the trunk of the family whence various genera have branched off since the Stephanian epoch. *Mesoleaia* is possibly a relic genus.

Distribution:—Lower Carboniferous to Lower Triassic.

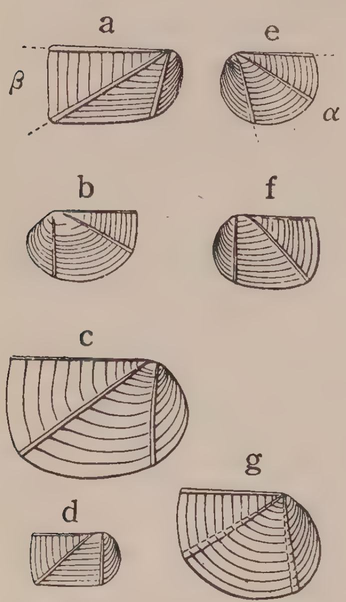

Figure 29. Some species of *Leaia* (after PRUVOST)

a. *Leaia leidyi* (JONES)
b. *Leaia trigonoides* MOYSEY
c. *Leaia tricarinata* MEEK and WORTHEN
d. *Leaia williamsoniana* JONES
e. *Leaia salteriana* JONES
f. *Leaia minima* PRUVOST
g. *Leaia baentschiana* BEYRICH

Genus *Eoleaia* KOBAYASHI, new genus

Diagnosis:—Leaiadidae with two radial ribs; carapace long; umbo terminal or subterminal on the straight dorsal margin; ventral margin a little arcuate or nearly straight.

Type:—*Pseudestheria leaiformis* RAYMOND.

Distribution:—Two species from Mississippian of Nova Scotia.

Genus *Leaia* JONES, 1863

Synonym:—*Hemicycloleaia* RAYMOND.

Diagnosis:—Leaiadidae with two carinae; in addition, the dorsal margin frequently thickened into a carina; their intersections with growth lines sometimes nodose; posterior outline sometimes limnadiform.

Remark:—Wide variations can be seen in *Leaia* with regard to carapace outline, or its height-length proportion and curvature and angulation of the margins, and the mode of carination and their disposition, length and curvature, and presence or absence of nodes on the carinae, by which many species are distinguished. These species are all bicarinate beside the dorsal margin which may be carinate or non-carinate. Growth lines are never as numerous as in Estherians. The sculpture in their interspace is so rarely preserved that no distinction can be made on that basis. *Leaia*, s. str. and *Hemicycloleaia* were designated respectively

for the forms with straight and arcuate ventral margin, but the difference is very gradual, which troubled RAYMOND when deciding whether *tricarinata* is a *Leaia* or a *Hemicycloleaia*. Therefore this distinction is not taken as ground for generic designation. In Pennsylvanian *Leaia acutangularis* and Stephanian *L. wettinensis* the anterior carina is rudimentary. The former is semi-elliptical and the latter semicircular. The carina is very weak also in some specimens of *Hemicycloleaia laevis*. (See RAYMOND, 1946, pl. 6, fig. 2).

Distribution:—Lower Carboniferous to Upper Permian. *Leaia salteriana* is a solitary early Carboniferous species. Subsequently the genus develops to reach its maximum and in fact there were more than 25 species in the late Carboniferous period. The next climax is the late Permian when more than 10 species are distinguishable in New South Wales. An undescribed species exists in South Africa, but the genus is unrepresented in Asia.

Genus *Monoleiolophus* RAYMOND, 1946

Diagnosis:—Leaiadidae with only one postero-ventral rib or carina.

Type:—*Monoleiolophus conemaughensis* KOBAYASHI (=*M. unicostatus* RAYMOND, non REED).

Remarks:—The carapace of the type species is more or less subquadrate. In subovate outline Russian *monocarinatus* is similar to Brazilian *unicostatus*. In the former, however, the postero-ventral carina is tuberculate and the interspace is coarsely punctate, while in the latter a fine regular reticulation covers the interspace and 14 to 16 concentric lamellose lines meet the radial at right angles and form imbrications in crossing it. In the latter the radial carina is commonly located closer to the dorsal margin than in the former.

Australian specimen (*Leaia* sp. undt., MITCHELL, 1925, pl. 42, fig. 13) seems to be monocarinate, but the specimen is unfortunately incomplete.

Distribution:—A species each from the Pennsylvanian of eastern North America and Upper Permian of Russia (Vetlugian), Brazil and possibly also New South Wales.

Genus *Discoleaia* KOBAYASHI, new genus

Diagnosis:—Leaiadidae with two carinae on the subelliptical valve.

Type:—*Leaia discoidea* MITCHELL, monotypic.

Remarks:—A blunt umbo is located less anteriorly than in many

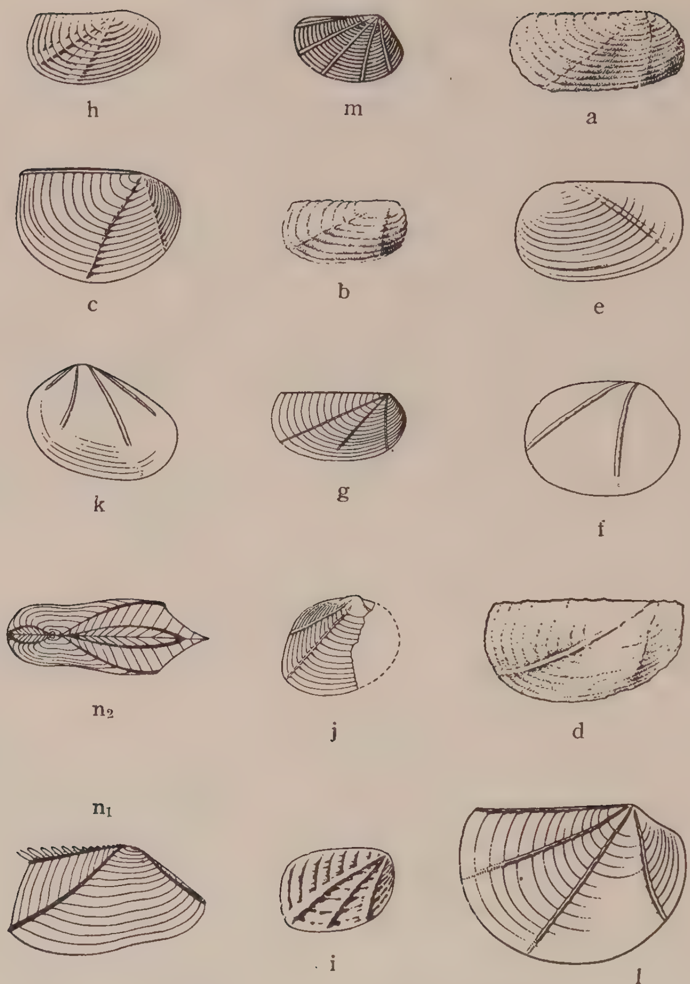

Figure 30. Some Leaian genera.

a. *Eoleaia leaiaformis* (RAYMOND) (after RAYMOND)
b. *Eoleaia laevicosta* (RAYMOND) (after RAYMOND)
c. *Leaia wettinensis* LASPEYRES
d. *Leaia acutangularis* RAYMOND (after RAYMOND)
e. *Monoleiolophus conemoughensis* KOBAYASHI
f. *Discoleaia discoidalis* (MITCHELL)
g. *Paraleaia klieveri* (GOLDENBERG) (after GUTHRÖL)
h. *Paraleaia fritschi* KOBAYASHI
i. *Paraleaia* (?) *weissi* FRITSCH
j. *Bileaia curta* (REED)
k. *Quadrileaia quadricarinata* (MITCHELL)
l. *Trileaia belmontensis* (MITCHELL)
m. *Mesoleaia nodosocostata* (GIEBEL) (after SCHMIDT)
n_{1-2}. *Acantholeaia regoi* ALMEIDA (after ALMEIDA)

other Leaians; anterior carina gently curved and thinning out near the ventral margin; the posterior carina nearly straight; median section larger than the anterior one; posterior section very small.

The specimen in fig. 22 on pl. 42, MITCHELL, 1925, is selected for the holotype, because it shows a perfect outline of the carapace. The other in fig. 6 on pl. 41 is strongly compressed laterally, if it belongs really to this species. The outline of the carapace is, however, not very much deformed in other species from the same locality. In both, concentric lines are not discernible.

Distribution:—Upper Permian of New South Wales.

Genus *Paraleaia* RAYMOND, 1946

Diagnosis:—Leaiadidae with a short groove or fold in the median section beside two carinae.

Type:—*Leaia leidyi* var. *klieveri* GOLDENBERG.

Remarks:—In the type species the carapace is long and the accessory radial groove extends from the umbo into the median section which is much wider than the other sections.

FRITSCH's *wettinensis* from Schladebach is quite different from LASPEYRES' in several aspects. In outline it looks nearer *klieveri* than *wettinensis*, but the two principal carinae are on the posterior side as in *Bileaia*. Because an accessory radial is inserted between the two like in *klieveri*, this species is taken for a new species of *Paraleaia*. *P. fritschi* is proposed for it. Its posterior outline tends to become limnadiform.

His *weissi* is quite different from the preceding ones in subquadrate outline as in *Leaia williamsoniana*. The margins except the anterior one are, however, gently arcuate and they meet without any angulation. The dorsal margin is not carinate. An accessory rib which becomes stronger ventrally bisects the median section. This looks like tricarinate *Trileaia*, but in this Australian genus a carina develops from the dorsal one. Therefore this is placed in *Paraleaia* rather than in *Trileaia*, considering also the difference of distribution.

Distribution:—Three species from the Stephanian of Germany.

Genus *Bileaia* KOBAYASHI, new genus

Diagnosis:—Leaiadidae with two close set posterior carinae.

Type:—*Leaia curta* REED.

Remarks:—It is not improbable that one more carina exists near

the anterior margin, although lack of the antero-ventral part in the type specimen makes it difficult to determine. Two carinae seen on the type specimen are close set to each other on the posterior side. On the large mesio-anterior section there are about 15 equidistant concentric raised lines. The lines are closer together in the section between the two carinae than in that section and are more numerous in the subdorsal section. Thus the lines in a section are apparently not in continuity with those of another section. The ribs swell up into scabrous elevations where they are crossed by the concentrics.

Distribution:—The type species from the Upper Permian of Brazil.

Genus *Quadrileaia* KOBAYASHI, new genus

Diagnosis:—Leaiadidae with two primary and two secondary carinae.

Type:—Leaia quadriradiata MITCHELL, monotypic.

Remark:—The two secondary carinae die out at about two-thirds the distance from the umbo to the margin. The two primaries also become weaker beyond two-thirds of the distance from the umbo. Concentric striae are perhaps 16 or more in number some of which in the outer one-third are evidently much stronger.

Distribution:—Upper Permian of New South Wales.

Genus *Trileaia* KOBAYASHI, new genus

Diagnosis:—Leaiadidae with three carinae beside a dorsal one; posterior carina usually shorter than the others.

Type:—Leaia belmontensis MITCHELL.

Remark:—The holotype specimen of *belmontensis* is 7.0 mm. long and 4.7 mm. high. The anterior carina is gently curved, but the others are straight; the posterior carina very strong, but may not reach the margin; 14 growth lines form frilling design in crossing the carinae. Although the median section is broader and the subdorsal section narrower than the two others, the difference is not very great.

Trileaia etheridgei, nov. (i.e. *Leaia* sp. undt. in fig. 21. pl. 43, MITCHELL, 1925) is not very different from the preceding in the disposition of the carinae, but the dorsal carina is strong, the ventral margin subparallel to the straight dorsal margin and the outline of the carapace subelliptical in this species. In outline this is similar to *Trileaia sulcata* nov. which is named after MITCHELL's *Leaia* sp. undt.

in fig. 20 on pl. 43. But in *sulcata* the groove runs very close to the strong dorsal carina.

In his *intermedia* the posterior radial carina is weak and extends no more than a half of the distance from the umbo to the posterior margin. It is a remarkable fact that a short or incipient subdorsal carina begins to branch off from the dorsal carina in *Leaia mitchelli* (MITCHELL, figs. 1–2 on pl. 41).

These five species as a whole tell the story of the development of the posterior carina and the change in the disposition of the three carinae caused by an addition of a new carina on the postero-dorsal side. The type species of this genus indicates the terminal form along this trend of development. The median carina of *Trileaia* must be equivalent to the posterior carina of *Leaia*.

Distribution:—Upper Permian of New South Wales.

Genus *Mesoleaia* KOBAYASHI, new genus

Diagnosis:—Leaiadidae with five nodose ribs regularly divergent from the umbo; some accessory riblets may be present; dorsal margin straight; outline dilates anteriorly.

Type:—Posidonia nodosocostata GIEBEL, monotypic.

Distribution—Buntsandstein of Germany.

Genus *Acantholeaia* ALMEIDA, 1950

Diagnosis:—Tricarinate Leaiadidae with a series of spines issuing from the intersections of the subdorsal carina with growth lines; median section very wide and medially depressed.

Type:—Acantholeaia regoi ALMEIDA, monotypic.

Distribution:—Upper Permian of Brazil.

CHAPTER VII

Summary and conclusion

Eliminating some 15 species whose references are erroneous or doubtful or whose names were merely listed, fossil Conchostracans in the 320 or so forms I have found so far, have been classified into 33 genera in 7 families as schematized in the 6th chapter. Among them 10 species are new. In addition new names have been given to 4 species on account of their homonymy. Generic references of these forms are, though very tentative for foreign ones, cited in the specific list except for a few to whose texts or plates I have not had access. More new forms can be expected from future explorations, especially in Central Asia and in southern continents, but at the same time a more careful comparative study may show some species to be synonyma to others or to be varieties or formae of some other species.

Our knowledge is still meager concerning the Lepidittidae and the history of the Conchostraca is a blank in the Middle Eo-Palaeozoic era.

Estherians are classified here into 14 genera in 3 families including 3 subfamilies in the Lioestheriidae and 2 subfamilies in the Limnadiidae. Here 12 genera or subgenera are eliminated by synonymy and *Quadriasumussia* is the sole new genus I could find. On the other hand 6 of 10 genera in the Leaiadidae are new. *Hemicycloleaia* is, however, synonymized with *Leaia* because of morphic continuity between the two genera. The Estheriellidae comprise 6 genera including 2 new ones.

The characteristics of the Estheriellidae and Leaiadidae are found in the radial ornaments and these families are distinguished principally by the difference in the stage of the carapace growth when the radial markings made their appearance.

Radial ornaments are seen in many fossil forms, but never in the living ones. It was really a great surprise to me to find so many aberrant forms in this fossil group, especially in the Leaiadidae and Estheriellidae. It is certain that the Conchostraca developed much more in the past than the present. A remarkable morphic radiance can be seen in the Leaiadidae in the phylogerontic stage.

The Estherian type of sculpture is known in the Leaiadidae and Rhabdostichidae and more obscurely in the Estheriellidae but not in

the Lepidittidae. The soft parts of these animals are known in the case of a few species of fossil Estherians which are similar to those of living ones in major aspect. Such well-preserved specimens are, however, exceedingly rare and more material is needed for a better understanding of Conchostracan palaeobiology. All other forms are represented simply by carapaces. The diagnosis of the Conchostraca is therefore based on carapace morphology.

Hoping to find some characteristic of the carapace which would serve to distinguish the Cyzicidae from the Leptestheriidae or one genus from the others, I took special pains in my study of carapace outlines, growth lines, sculptures and others, but the conclusion I was forced to reach was that it is practically impossible to distinguish these families and genera on the basis of carapace only.

Cyclestherioides comprising a great variety merges with *Estherites* and certain other genera in the outline of the carapace. Therefore the Cyclestheriidae and the above-mentioned two neontological families must be placed in the Lioestheriidae in palaeontology and any generic name of those three families can be applied to fossil Estherians.

Some fossil genera are referred tentatively to the Limnadiidae or Lynceidae because of their similarity in one or other aspect. But the Estheriininae and Vertexiinae are erected in the Limnadiidae to distinguish the fossil genera from the living ones which are combined in the new subfamilies, because little is known actually of the relation between the fossil and living genera.

In the Conchostraca two valves are tightly fused along the dorsal margin. They consist of a thick outer carapace and a thin inner membrane which is an extension of the cuticle of the body through the umbonal area. I could not get much information on the structure and growth of the carapace, but it is evident that a series of growth bands records carapace growth, because the carapace is kept at the time of moulting except in the Lynceidae. Therefore the change in carapace outline and the relative position of the umbo through growth are important subjects for a phylogentical study.

Estherian sculpture on the test can be classified into various types, but little is as yet known of their biological meaning and before it can be used as a basis for classification more knowledge on the hypodermis and its secretion of the carapace material is necessary.

The sculpture can certainly exhibit important characteristics distinguishing the Conchostracan carapace from other similar shells.

But to classify the Conchostracan into families and genera, outline and convexity of the carapace, position of the umbo, presence or absence of growth lines on the carapace or on the umbo and of radial ornaments and spines constitute more important distinguishing characteristics than the sculpture.

As morphic differences in the carapace between the male and the female are not marked in living Estherians, it is probable that such differences were not great in fossil ones.

Polymorphism due to endemism and mutation, coupled with sexual dimorphism, make it difficult to grasp the specific concepts of fossil Estherians.

Estherians live now in shallow pools in the early summer. Their life cycle is completed in a few weeks, and they spend the rest of the year as eggs which are quite durable when locked within egg capsules. The distribution of Estherian species is mostly not very extensive.

Their dispersal is effected by egg capsules and carapaces being transported by wind or water current. Therefore one must always bear in mind the possibility that a thanatocoenosis is frequently different entirely from a biocoenosis. Although fossil Conchostracans do not occur in very coarse rocks or in off-shore marine sediments, they are contained in various kinds of sediments in limnic and paralic facies and rarely in neritic facies. Therefore they can be used for stratigraphic correlation of heteropic formations. The occurrence of *Paraleaia* and *Estheriella*, for example, are restricted respectively to the Upper Carboniferous and Lower Triassic of Europe. There are some species already in use as leading fossils for the stratigraphy of the Coal Measures in Europe.

A great difficulty in their use as guide fossils, however, lies in the difficulty of their specific identification. This is due not only to the insignificance of the aspects but also to the easy deformation of the carapace on account of its thinness and flexibility. Carapaces are deformed primarily by the compaction of the mother rocks and secondarily when the formation containing the fossil is deformed. Therefore a fossil-coenosis can be still further different from a thanatocoenosis. Because of their bearing on preservation, it is important to study not only deformation but also fossilization and defossilization as well as their differential processes between Conchostracans and other fossils having thicker or calcareous shells.

Conchostracans as individuals are of great interest to palaeontologists, but aspects of a fauna in which they are assembled are not less attractive to scientists because size variation of the carapace and morphic diversity of the fauna reveal adaptation of the Conchostracans to environment.

A statistical survey of the distribution of living Estherian species shows that optimum condition for their propagation and growth is found in inland basins in warm temperate zones of 20 to 30 degrees C. in hot season. There one can see a large number of species. Their carapaces grow larger. In fact carapaces are all small in the few living species in the tundra region the carapace size may thus provide us with a key to the solution of questions in palaeoclimatology. Climatic change in the Mesozoic era in Eastern Asia can be greatly elucidated by the aid of Estherians.

The Estherian faunas in Eastern Asia can be classified into two kinds. One is the synorogenic fauna in the peri-continental zone in which many aberrant indigenous forms are contained. Accordingly morphic diversity is high in this kind of fauna. The other is the interorogenic fauna in the intracontinental terrain which consists of a few species, but polymorphism is high in extensively distributing ones. The degree of morphic diversity in an Estherian fauna is not only indicated by the number of species or genera but can also be measured by the angle of morphic diversity as defined before.

The two kinds of fauna are combined in a suit and the biocycle indicated by such a suit reveals a parallel to the orogenic cycle. The development of Estherian faunas in Eastern Asia is quite intimately related to crustal movements in the same region. This was indeed a revelation, something which I did not even dream of when I started this study. The anorogenic type of faunas on kratonic masses is of course more related to the interorogenic than to the synorogenic type. Thus the aspect of the Estherian or Conchostracan fauna differs according to tectonic province. Therefore they can be morphic indices to palaeoclimatology and palaeo-ecology on the one side and to palaeo-orography and palaeo-hydrography on the other.

Although no non-marine Conchostracan has yet been discovered from the Antarctic circle or in Greenland, they are known to occur extensively in all continents. Non-marine Conchostracans appeared immediately after the paroxysm in the Caledonian orogenic cycle. Marine Lepidittidae are possibly ancestral to them. The Devonian

Conchostracans are almost all distributed in the Old Red *Gürtel* of Eur-America. Distribution did not change much in the early Carboniferous, but by the latter part they had already reached Eastern Asia and probably also South Africa. At the same time they developed greatly in the *Kohlengürtel* of Eur-America.

In the Permian period they spread all over the northern and southern continents when the number of species and genera attained their maximum. In the total number of species the Triassic Estherians are not much different from the Permian ones, but they declined abruptly in Jurassic and later. The Leaiadidae and Estheriellidae had died out completely by the end of the Triassic period.

In Eastern Asia, however, Estherians developed after the Middle Triassic epoch. Conchostracans flourished in the late Permian and early Triassic in Russia and central Siberia and in the late Carboniferous in the *Kohlengürtel* of Eur-America. Thus the rise and fall of the Conchostraca in the northern continents are reciprocal between Eur-America and Asia. The shifting of the center of their distribution matches that of the orogenic storm from the Atlantic to the Pacific side.

As palaeontological records vanish with the late Cretaceous Sungari fauna, what happened to this creature in the Tertiary period is unknown, although undoubtedly it must have led an insignificant existence at that time. In view of the strong influence of glaciers on the dispersal of recent Estherians from the Mediterranian region to Eastern Asia, the Great Ice Age must have been a powerful factor in the phyletic rejuvenescence of the Conchostraca.

Although the conclusion introduced here will require more time before it can be theorized, the salient results brought to light have been summarized above. I have also mentioned the important questions which arose in my mind in the course of this study. Their solution is left to the Conchostracan students of the future.

Chapter VIII. List of genera and species of the fossil Conchostraca

Two alphabetical lists, generic and specific, are provided here for the convenience of taxonomists. Some of the genera or species which have been eliminated from the Conchostraca are included in the lists. These lists, it is hoped, are complete, but there may be some genera and species which I have overlooked, especially from among northern Eurasiatic faunas.

In the list of species the specific name and its occurrence are connected with the present determination by dashes. As to generic descriptions or discussions the reader is referred to the index which follows the postscripts.

1. Alphabetical list of fossil Conchostracan genera, subgenera and related ones, their type species being cited in brackets

Acantholeaia ALMEIDA, 1950	(*Acantholeaia regoi* ALMEIDA, 1950)
Anomalonema RAYMOND, 1946	(*Estheriella reumauxi* PRUVOST, 1911)
Asmussia PACHT, 1849	(*Asmussia membranacea* PACHT, 1849)
Bileaia KOBAYASHI, nov.	(*Leaia curta* REED, 1929)
Congestheriella KOBAYASHI, nov.	(*Estheriella lualabensis* LERICHE, 1913)
Cornia LUTKEVICH, 1938	(*Cornia papillaria* LUTKEVICH, 1937)
Cyclestherioides RAYMOND, 1946	(*Estheria lenticularis* MITCHELL, 1927)
Dadaydedeesia RAYMOND, 1946	(*Estheriella radiata* (SALINA) var. *multiradiata* JONES, 1915)
Diaphora NOVOZHILOV, 1946, non STEPHENS, 1828	(*Diaphora tuberculata* NOVOZHILOV, 1946)
Diaplex NOVOZHILOV, 1946	(*Diaplex tigjanensis* NOVOZHILOV, 1946)
Discoleaia KOBAYASHI, nov.	(*Leaia discoidea* MITCHELL, 1925)
Echinestheria MARLIÈRE, 1950	(*Estheria* (*Echinestheria*) *marimbensis* MARLIÈRE, 1950)
Eoleaia KOBAYASHI, nov.	(*Pseudestheria leaiformis* RAYMOND, 1946)
Erisopsis RAYMOND, 1946	(*Erisopsis belli* RAYMOND, 1946)
Estheriella WEISS, 1875	(*Estheriella costata* WEISS, 1875)
Estheriellites BOCK, 1953	(*Estheriella elliptoidea* BOCK, 1946)
Estheriina JONES, 1891	(*Estherina bresiliensis* JONES, 1897)

Estheriopsis RUSCONI, 1948	(*Estheriopsis bayensis* RUSCONI, 1948)
Estherites KOBAYASHI, and HUZITA, 1943	(*Estheria mitsuishii* KOBAYASHI and HUZITA, 1942)
Euestheria DEPÉRET and MAZERAN, 1912	(*Posidonia minuta* VON ZIETEN, 1833)
Fordilla BARRANDE, 1881	(*Fordilla troyensis* BARRANDE, 1881)
Hemicycloleaia RAYMOND, 1946	(*Hemicycloleaia laevis* RAYMOND, 1946)
Howellites BOCK, 1953	(*Howellites princetonensis* BOCK, 1953)
Leaia JONES, 1862	(*Cypricardinia leidyi* LEA, 1855)
Lepiditta MATTHEW, 1886	(*Lepiditta alata* MATTHEW, 1886)
Limnestheria WRIGHT, 1928	(*Limnestheria ardra* WRIGHT, 1928)
Lioestheria DEPÉRET and MAZERAN, 1912	(*Lioestheria lallyensis* DEPÉRET and MAZERAN, 1912)
Mesoleaia KOBAYASHI, 1953	(*Posidonia nodosocostata* GIEBEL, 1857)
Metaleaia KOBAYASHI, 1952	(*Praeleaia triassiana* CHERNYSHEV, 1934)
Modioloides WALCOTT, 1889	(*Modioloides prisca* WALCOTT, 1887)
Monoleiolophus RAYMOND, 1946	(*Monoleiolophus unicostatus* RAYMOND, 1946)
Nyasestheriella KOBAYASHI, nov.	(*Estheriella nyasana* NEWTON, 1910)
Orthothemos RAYMOND, 1946	(*Estheria draperi* JONES and WOODWARD, 1894)
Palaeestheria BERNARD, 1929	(*Estheria anomala* JONES, 1901)
Palaeolimnadia RAYMOND, 1946	(*Estheria wianamattensis* MITCHELL, 1927)
Palaeolimnadiopsis RAYMOND, 1946	(*Palaeolimnadiopsis carpenteri* RAYMOND, 1946)
Paraleaia RAYMOND, 1946	(*Leaia klieveri* GOLDENBERG, 1873)
Pemphicyclus RAYMOND, 1946	(*Pemphicyclus laminatus* RAYMOND, 1946)
Polygrapta NOVOZHILOV, 1946	(*Polygrapta chatangensis* NOVOZHILOV, 1946)
Praeleaia LUTKEVICH, 1929	(*Prealeaia quadricarinata* LUTKEVICH, 1929)
Pseudestheria RAYMOND, 1946	(*Pseudestheria brevis* RAYMOND, 1946)
Pseudoleaia KOBAYASHI, 1952	(*Estheria rectangula* YOKOYAMA, 1894)
Quadriasmussia KOBAYASHI, nov.	(*Estheria hercynica* KUMMEROW, 1939)
Quadrileaia KOBAYASHI, nov.	(*Leaia quadrata* MITCHELL, 1925)
Rhabdostichus RAYMOND, 1946	(*Estheria pulex* CLARKE, 1882)
Schizodiscus CLARKE, 1888	(*Schizodiscus capsa* CLARKE, 1888)
Trileaia KOBAYASHI, nov.	(*Leaia belmontensis* MITCHELL, 1925)
Vertexia LUTKEVICH, 1941	(*Vertexia tauricornis* LUTKEVICH, 1941)

2. Alphabetical list of fossil Conchostracan species, varieties, formae and allied ones

acutangularis RAYMOND, 1946, *Hemicycloleaia*; Penn.; N. America (Rhode Island) ....*Leaia*

adamsi JONES, 1870, *Estheria*; Carbon. (Coal Measures); Wales ....*Euestheria*

aequale LUTKEVICH, 1937, *Estheria*; Trias. (Vetlug, Maltsévo); Russia, Siberia (Kuznetsk, Tungusska) ....*Lioestheria*

alata MATTHEW, 1886, *Lepiditta*; Cambrian (Mid.); N. America (New Brunswick) ....*Lepiditta*

alberti VOLTZ, 1837, *Posidonia*; Trias. (Buntsandstein); Germany (Elsace, Franken) ....*Euestheria*

alta RAYMOND, 1646, *Pseudestheria*; Miss. (Cheverie); N. America (Nova Scotia) ....*Asmussia*

ameliae SALINAS, 1897, *Estheria*; Trias. (Carnic); Sicily....*Posidonia* (?)

amurensis CHERNYSHEV, 1930, *Estheria*; Cretaceous (Tsagoiana); Siberia (Seja), Manchuria (?) ....*Euestheria*

anabarensis NOVOZHILOV, 1946, *Estheria*; Trias (Anisic); Siberia (Chatanga) ....*Lioestheria*

anchietai TEIXEIRA, 1947, *Estheria* (*Euestheria*); Perm (Up.); Africa (Angola) ....*Euestheria*

andrewsi JONES, 1891, *Estheria*; Cretaceous (Wealden); England ....*Lioestheria*

angolensis LERICHE, 1932, *Estheria mangaliensis*; Trias. (Up.); Africa (Angola, Congo) ....*Euestheria angolensis*

angulata LUTKEVICH, 1941, *Estheria*; Perm (Tatar.); Russia..*Lioestheria*

anomala JONES, 1901, *Estheria*; Cretaceous (Low.); S. Africa ....*Lioestheria*

antecrenulus CLEAVES, 1935, *Schizodiscus*; Devon. (Moscow sh.); N. America (Pa.) ....*Schizodiscus*

ardra WRIGHT, 1928, *Limnestheria*; Carbon. (Coal Measures); Ireland ....*Limnestheria*

arguta NOVOZHILOV, 1946, *Estheria aquale*; Trias. (Anisic); Siberia (Chatanga) ....*Lioestheria*

aricensis JONES, 1897, *Estheria*; Carbon. (?); Peru ....*Euestheria*

articulata MATTHEW, 1894, *Lepiditta*; Cambrian (Mid.); N. America (New Brunswick) ....*Lepiditta* (?)

asanoi KOBAYASHI and KUSUMI, 1953, *Estherites*; Cretaceous (Kyöngsang); Manchuria ....*Euestheria*

ashleyi RAYMOND, 1946, *Hemicycloleaia*; Penn. (Conemaugh); N. America (Pa.) ....*Leaia*

asteroides JONES, 1897, *Estheriina*; Cretaceous (Bahian); Brazil ....*Estheriina*

atsuensis KOBAYASHI, 1952, *Estherites*; Trias. (Carnic); Japan ....*Estheriina*
autunensis RAYMOND, 1946, *Euestheria*; Perm. (Rothliegend); France ....*Euestheria*
avonensis RAYMOND, 1946, *Leaia*; Miss.; N. America ......nom. nud.
baentschiania BEYRICH, 1864, *Leaia leidyi*; Carbon. (Up.); Germany, Spain ....*Leaia baentschiana*
barbosai ALMEIDA, 1950, *Bairdestheria*; Rhaetic (or Lias.); Brazil ....*Euestheria*
barroisei RAYMOND, 1946, *Leaia*; Carbon. (Westphalian); Belgium ....*Leaia*
bayensis RUSCONI, 1948, *Estheriopsis*; Trias.; Argentina....*Estheriopsis*
beanschi WATERLOT, 1934, *Leaia*; ....*Leaia baentschiana*
beinertiana JONES, 1862, *Estheria striata*; Carbon. (Westphalian); Germany, (Silesia), England ....*Euestheria beinertiana*
bellambiensis MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Lioestheria*
belli RAYMOND, 1946, *Erisopsis*; Miss. (Cheverie); N. America (Nova Scotia) ....*Asmussia* (?)
belmontensis MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Trileaia*
belmontensis MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Lioestheria* (?)
berryi BOCK, 1953, *Howellites*; Trias. (Newark); N. America (N. Carolina) ....*Euestheria*
binneyana JONES, 1862, *Estheria striata*; Carbon. (Coal Measures); England ....*Euestheria binneyana*
blackstonensis RAYMOND, 1946, *Pseudestheria*; Penn.; N. America (Rhode Island) ....*Cyclestherioides*
boltoni RAYMOND, 1946, *Hemicycloleaia*; Carbon. (Westphalian); England ....*Leaia*
borgesi TEIXEIRA, 1943, *Estheria*; Stephanian or Perm.; Africa (Mozambique) ....*Lioestheria*
bornhardti JANENSCH, 1927, *Estheriella*; Trias. (Up.); Africa (Tanganika) ...."*Estheriella*"
bresiliensis JONES, 1897, *Estheriina*; Cretaceous (Bahian); Brazil ....*Estheriina*
brevis RAYMOND, 1946, *Pseudestheria*; Perm. (Low.); N. America (Okla.) ....*Lioestheria*
bristolensis RAYMOND, 1946, *Leaia*; Carbon. (Westphalian); England ....*Leaia*
brodieana JONES, 1863, *Estheria minuta*; Trias. (Rhaetic); England, Scotland, Germany ....*Euestheria*
brodiei MARLIÈRE, 1948, non *brodieana* JONES, *Estheria (Euestheria) minuta*; Trias. (Low.); Africa (Congo) ....*Euestheria*, sp. nov. (?)
buchoti PÉNEAU, 1937, *Estheria (Euestheria)*; Up. Gotlandian or Devon.; France ....*Rhabdostichus*

carneiroi TEIXEIRA, 1942, *Estheria* (*Euestheria*); Carbon. (Stephanian); Portugal ....*Euestheria*
carpenteri RAYMOND, 1946, *Palaeolimnadiopsis*; Perm. (Wellington); N. America (Okla.) ....*Palaeolimnadiopsis*
caspa CLARKE, 1888, *Schizodiscus*; Devon; N. America (N.Y.)..*Schizodiscus*
cebennensis GRAND'EURY, 1890, *Estheria*; Carbon. (Up.); France, Russia (Donetz), Bohemia, Portugal ....*Euestheria*
cellulata LUTKEVICH, 1941, *Estheria*; Perm. (Tatar.); Russia..*Lioestheria*
chatangensis NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
chernyshevi RAYMOND, 1946, *Pemphicyclus*; Carbon. (Westphalian); Russia (Donetz) ....*Cornia*
chii KOBAYASHI and KUSUMI, 1953, *Estherites middendorfii*; Jurassic (Jehol); Manchuria, Korea ....*Euestheria*
chilensis JONES, 1897, *Estheria* ....*Cyclestherioides molesta*
chilensis PHILLIPI, 1887, *Estheria* (?); Chili (Lebu) ....*Cyclestherioides*
cicatricosta NOVOZHILOV, 1946, *Estheria*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
ciofaloi GEMMELLARO, 1882, *Estheria*; Trias. (Carnic); Sicily ....*Posidonia* (?)
circularis BOCK, 1946, *Estheriella*; Trias. (Newark); N. America (Pa.) ....*Euestheria*
clarkei RAYMOND, 1946, *Asmussia*; Devon. (Mid.); N. America (N.Y.) ....*Asmussia*
coghlani COX, 1881, *Estheria*; ....nom. nud.
coghlani ETHERIDGE, 1888, *Estheria*; Trias.; Australia (NSW.) ....*Euestheria* (?)
collinsi MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Leaia*
columbianus BOCK, 1953, *Howellites*; Rhaetic (or Lias.); S. America (Columbia) ....*Euestheria*
compta MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Leaia*
concentrica BEAN, 1836, *Estheria*; Jura.; England (Yorkshire) ....*Estherites*
conemaughensis KOBAYASHI, nov. *Monoleiolophus*; Penn.; N. America (Pa.) ....*Monoleiolophus*
contorta RUSCONI, 1948, *Pseudestheria*; Rhaeto-Lias; Argentina (Mendoza) ....*Cyclestherioides*
costata WEISS, 1875, *Estheria* (*Estheriella*); Trias. (Buntsandstein); Germany (Franconia, Saxony) ....*Estheriella*
crassa LUTKEVICH, 1929, *Estheria*; Devon. (Mid.); Esthonia, Russia (Leningrad Region) ....*Euestheria*
curta MATTHEW, 1886, *Lepiditta*; Cambrian (Mid.); N. America (New Brunswick) ....*Lepiditta*
curta REED, 1929, *Leaia*; Perm. (Up.); Brazil ....*Bileaia*
cuyanensis RUSCONI, 1946, *Rhabdostichus* (?); Cambrian (Mid.); Argentina ....(?)

cyanea FRITSCH, *Estheria*; Perm.; Bohemia ....(?)
cycloides KOBAYASHI, 1950, *Estherites*; Rhaeto-Lias (?); Korea ....*Cyclestherioides*
cymruensis RAYMOND, 1946, *Leaia*; Carbon. (Coal Measures); Wales ....*Leaia*
Cyzicus sp. HAUGHTON; Trias. (Lubilash); Africa (Congo)..*Euestheria* (?) sp.
dahurica CHERNYSHEV, 1930, *Estheria*; Jura. (Turga); Siberia (Transbaikalia) ....*Estherites* (?)
daja CHERNYSHEV, 1940, *Estheria*; Jura.; Siberia (Transbaikalia) ....*Euestheria*
dawsoni JONES, 1870, *Estheria*; Miss. (Cheverie); N. America (Nova Scotia) ....*Euestheria*
dawsoni PACKARD, 1881, *Estheria* ....Teleostern scale (?)
densicostata CHERNYSHEV, 1926, *Estheriella*; Carbon. (Westphalian); Russia (Donetz) ....*Anomalonema* (?)
destombesi DEFRETIN and FAUVELT, 1951, *Estheria*; Rhaeto-Lias.; Africa (Morocco) ....*Euestheria* (?)
deverta NOVOZHILOV, 1946, *Estheria*; Trias. (Anisic); Siberia (Chatanga) ....*Estherites*
diensti GROSS, 1934, *Estheria*; Devon. (Low.); Germany (Eifel) ....*Lioestheria*
discoidea MITCHELL, 1925 *Leaia*; Perm. (Up.); Australia (NSW.) ....*Discoleaia*
draperi JONES and WOODWARD, 1894, *Estheria*; Trias. (Cave sandstone), Africa (Cape Colony, ? Kongo) ....*Estherites*
drummi GUTHÖRL, 1931, *Estheria*; Perm. (Zechstein); Germany ....*Cornia* (?)
eichwaldi NETSCHAJEW, 1894, *Estheria*; Perm. (Kazan.); Russia ....*Euestheria*
eifelensis RAYMOND, 1946, *Palaeolimnadiopsis* (?); Devon. (Low.); Germany (Eifel) ....*Lioestheria diensti*
elegantula LUTKEVICH, 1941, *Estheria*; Devon. (Up.); Russia (Low. Volga) ....*Lioestheria* (?)
elliptica DUNKER, 1843, *Estheria*; Cretaceous (Neocom.); Germany ....*Euestheria*
elliptica MITCHELL, 1925, *Leaia*; Perm. (Belmont); Australia (NSW.) ....*Leaia*
elliptoidea BOCK, 1946, *Estheriella*; Trias. (Newark); N. America (Pa.) ....*Euestheria*
elongata CHERNYSHEV, 1926, *Estheria* (*Euestheria*); Carbon. (Westphalian); Russia (Donetz) ....*Euestheria*
elongata KOBAYASHI and KUSUMI, 1953, *Estherites middendorfii*; Jura. (Jehol); Manchuria ....*Euestheria*
elongata NETSCHAJEW, 1894, *Estheria*; Perm. (Tatar.); Russia ....*Lioestheria*
emmonsi RAYMOND, 1946, *Pseudestheria*; Trias. (Newark); N. America (Va.) ....*Euestheria*

endoi KOBAYASHI and KIDO, 1945, *Estherites*; Cretaceous (Talatzu); Manchuria ....*Estherites*
eos EICHWALD, 1846, *Cyclas* ....*Cyclestherioides exigua*
Estheria sp. ind. HAYNES, 1913, (pars) ....*Cyclestherioides blackstonensis.*
Estheria sp. KROTOW, 1888 ....Pelecypod
etheridgei KOBAYASHI, nov. *Trileaia*; Perm. (Up.); Australia (NSW.) ....*Trileaia*
excentrica LUTKEVICH, 1941, *Estheria*; Devon. (Up.); Russia (Timan, Low. Volga) ....*Asmussia*?
exigua EICHWALD, 1846, *Posidonomya*; Perm. (Kazan.); Russia ....*Cyclestherioides*
exigua LUTKEVICH, 1941, non EICHWALD, *Estheria* ....*Lioestheria lutkevichi*
expansa JONES, 1897, *Estheriina*; Cretaceous (Bahian); Brazil ....*Estheriina*
exsecta NOVOZHILOV, 1946, *Estheria*; Trias. (Anisic); Siberia (Chatanga) ....*Euestheria*
extuberata JONES and WOODWARD, 1890, *Estheriina*; Perm.; Germany ....*Estheriina* (?)
forbesii by IMLAY, 1941, *Estheria* aff.; Jura.; N. America (Louisiana) ....*Euestheria* sp. nov. (?)
forbesii JONES, 1863, *Estheria*; Rhaetic (?); Argentina (Mendoza) ....*Euestheria*
foveolata CHERNYSHEV, 1930, *Estheria*; Rhaeto-Lias.; Siberia (Irkutsk, Transbaikalia) ....*Euestheria*
freysteini GEINITZ, 1885, *Cardinia*; Carbon. (Up.); Germany ....*Estheriina* (?)
fritschi KOBAYASHI, nov., *Bileaia*; Carbon. (Stephanian); Germany ....*Paraleaia*
fukiensis GRABAU, 1924, *Estheria*; Perm. (Up.); China (Fukien) ....*Euestheria*
gabonnensis MARLIÈRE, 1950, *Estheria* (*Pemphicyclus*); Stephanian or Perm.; Africa (Zambezi) ....*Cornia*
geinitzi JONES and WOODWARD, 1893, *Estheria*; Perm. (Rothliegend); Germany ....*Euestheria* (?)
gemmellaroi SALINAS, 1897, *Estheria*; Trias. (Carnic); Sicily ....*Posidonia* (?)
germari BEYRICH, 1857, *Posidonia*; Trias. (Buntsandstein); Germany ....*Euestheria*
glabra, MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Estheriina*
glenleensis MITCHELL, 1927, *Estheria*; Trias. (Wianamatta) Australia (NSW.) ....*Estheriina*
grebeana JONES and WOODWARD, 1893, *Estheria geinitzi*; Perm.; Germany ....*Euestheria* (?)
greyi JONES, 1878, *Estheria*; Trias. (Beaufort); S. Africa ..*Cornia* (?)
grossi KOBAYASHI, nov., *Cyclestherioides*; Devon. (Low.); Germany ....*Cyclestherioides*

gutta LUTKEVICH, 1937, *Estheria*; Trias. (Vetlug., Maltsévo); Russia, Siberia (Kuznetsk, Tungusska) ....*Lioestheria*
halobiformis KOBAYASHI and KUSUMI, 1953, *Estherites*; Cretaceous (Kyöngsang); Manchuria ....*Euestheria*
hauchecornei FRITSCH, 1900, *Estheria*; Carbon. (Up.); Germany ....*Euestheria*
hausmanni BEYRICH, (in KITTL, 1912) *Estheria*; Trias. (Rhaetic); Germany (Hannover) ....Not Estherian(?)
haynesi RAYMOND, 1946, *Hemicycloleaia*; Penn. (Conemaugh); N. America (Rhode Island) ....*Leaia*
heckeri CHERNYSHEV, 1930, *Estheria*; Rhaeto-Lias. (Trubachevo); Siberia (Transbaikalia, Yenissei) ....*Estherites*
hercynica KUMMEROW, 1939, *Estheria*; Carbon. (Low.); Germany (Harz) ....*Quadriasmussia*
herriana GUTHÖRL, 1934, *Leaia*; Carbon. (Stephanian); Germany (Saar) ....*Leaia*
hindei JONES, 1891, *Estheria*; Trias. (Newark); N. America (Pa.) ....*Euestheria*
huzitai KOBAYASHI and KIDO, 1945, *Estherites kyöngsangensis*; Cretaceous (Naktong); Korea ....*Euestheria*
ignota NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Cornia* (?)
inornata RAYMOND, 1946, *Lioestheria*; Trias. (Newark); N. America (Va.) ....*Lioestheria*
intaminata NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
intermedia CHI, 1931, *Estheria elliptica*; Up. Jura. or Low. Cretaceous; Central China ....*Euestheria intermedia*
intermedia KOBAYASHI and KUSUMI, 1953, *Estherites middendorfii*; Jura. (Jehol); Manchuria, Korea ....*Euestheria*
intermedia MITCHELL, 1945, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Trileaia*
ipsviciensis MITCHELL, 1927, *Estheria*; Trias. (Up.); Australia (Queensland) ....*Euestheria*
janenschi KOBAYASHI, nov., *Cyclestherioides*; Jura. (Perbeck); Africa (Tanganika) ....*Cyclestherioides*
jeholensis KOBAYASHI and KUSUMI, 1953, *Estherites middendorfii*; Jura. (Jehol); Manchuria, Transbaikalia ......*Euestheria*
jonesi RAYMOND, 1946, *Palaeolimnadiopsis*; Miss.; N. America (Nova Scotia) ....*Palaeolimnadiopsis*
kansuensis CHI, 1932, *Estheria*; Jura. (Jehol); N. China....*Euestheria*
kantoensis KOBAYASHI and KIDO, 1945, *Estherites*; Cretaceous (Talatzu); Manchuria ....*Palaeolimnadiopsis*
kargalensis NETSCHAJEW, 1894, *Leaia*; Perm. (Kazan.), Russia ....*Leaia*
karpinskiana JONES, 1883, *Estheria minuta*; Trias. (Rhaetic); Siberia (E. Ural) ....*Euestheria karpinskiana*

kasaiensis MARLIÈRE, 1950, *Estheria (Bairdestheria)*; Trias. (Low.); Africa (Congo) ....*Euestheria*
kawasakii OZAWA and WATANABE, 1923, *Estheria*; Trias. (Mine, Daido); Japan, Korea ....*Euestheria*
khinganensis KOBAYASHI, 1950, *Estherites*; Jura. (Lias. ?); Manchuria ....*Asmussia*
kidoi KOBAYASHI, nov. *Euestheria*; Rhaeto-Lias. (?); Korea ....*Euestheria*
klieveri GOLDENBERG, 1873, *Leaia leidyi*; Carbon. (Stephanian); Germany ....*Paraleaia klieveri*
klieveriana GOLDENBERG, 1877, *Leaia* ....*Leaia klieveri*
kobozevi LUTKEVICH, 1941, *Estheria*; Perm. (Tatar.); Russia ....*Estherites*
koreanica OZAWA and WATANABE, 1923, *Estheria*; Trias. (Carnic); Japan, Korea ....*Cyclestherioides*
kotahensis JONES, 1862, *Estheria*; Jura. (Kota); India ......*Euestheria*
krystofovichi CHERNYSHEV, 1930, *Estheria*; Rhaeto-Lias.; Siberia (Ussuri) ....*Lioestheria*
kubaczeki VOLZ, 1896, *Estheria*; Trias. (Muschelkalk); Germany (Silesia) ....*Lioestheria*
kusumi KOBAYASHI, nov., *Euestheria*; Rhaeto-Lias. (?); Korea ....*Euestheria*
kutsangkouensis KOBAYASHI and KUSUMI, 1953, *Estherites nengkiangensis*; Cretaceous (Kyöngsang); Manchuria ....*Euestheria*
kwantoensis MATSUZAWA, in SAITO, 1933, *Estheria* ....nom. nud.
kyöngsangensis KOBAYASHI and KIDO, 1945, *Estherites*; Cretaceous (Naktong); Korea ....*Euestheria*
laevicosta RAYMOND, 1946, *Leaia*; Miss.; Canada (Nova Scotia) ....*Eoleaia*
laevis RAYMOND, 1946, *Hemicycloleaia*; Penn. (Conemaugh); N. America (Pa.) ....*Leaia*
lallyensis DEPÉRET and MAZERAN, 1912, *Estheria*; Perm. Rothliegend); France ....*Lioestheria*
laminatus RAYMOND, 1946, *Pemphicyclus*; Perm.; N. America (Okla.) ....*Cornia*
laptewi NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
lata MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Euestheria*
latissima MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Leaia*
latus KOBAYASHI and KUSUMI, 1953, *Estherites proamurensis*; Cretaceous (Kyöngsang); Manchuria ....*Euestheria lata*
laxa NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
laxitecta JONES, 1878, *Estheria*; Trias. (Keuper); Germany (Franconia) ....*Euestheria*
laxitecta SANDBERGER, 1871, *Estheria* ....nom. nud.

Leaia sp. indt. DAWSON, 1868; Miss.; Canada (Nova Scotia) ....*Leaia* (aff. *subquadrata*)
Leaia sp. indt. MITCHELL, 1925; Perm. (Up.); Australia (NSW.) ....*Monoleiolophus* (?) sp.
Leaia sp. indt. MITCHELL, 1925, pl. 43, fig. 20, ...*Trileaia sulcata.*
Leaia sp. indt. MITCHELL, 1925, pl. 43, fig. 21 ....*Trileaia etheridgei*
leaiaformis RAYMOND, 1946, *Pseudestheria*; Miss. (Cheverie); N. America (Nova Scotia) ....*Eoleaia*
lebombensis RENNIE, 1937, *Palaeestheria*; Jura. (Lias.); Africa (Mozambique) ....*Euestheria*
leidyi LEA, 1855, *Cypricardinia*; Miss. (Cheverie, Mauch Chunk); N. America (Nova Scotia, Pa.) ....*Leaia*
lenticularis MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Cyclestherioides*
leonense RUSCONI, 1948, *Pseudestheria*; Rhaeto-Lias.; Argentina (Mendoza) ....*Cyclestherioides*
lerichei MARLIÈRE, 1950, *Estheria* (*Euestheria*) ....*Estherites angolensis*
lewisii JONES, 1890, *Estheria*; Trias. (Newark); N. America (Pa.) ....*Euestheria* (?)
limbata GOLDENBERG, 1877, *Estheria*; Carbon. (Stephanian); Germany ....*Cornia* (?)
limbata NOVOZHILOV, 1946, *Polygrapta* ....*Cornia* (?) *novozhilovi*
lineata LUTKEVICH, 1941, *Estheria*; Perm. (Tatar.); Russia ..*Lioestheria*
lineata WEISS, 1875, *Estheriella*; Trias. (Buntsandstein); Germany ....*Estheriella*
linguiformis MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Estheriina*
loczyi FRECH, 1905, *Estheria*; Trias. (Cassian), Hungary (Bakony) ....*Posidonia* or *Halobia* (?)
lualabensis LERICHE, 1913, *Estheriella*; Perm. (Up.); Africa (Congo) ....*Congestheriella*
lutkevichi KOBAYASHI, nov., *Lioestheria*; Perm. (Kazan.); Russia ....*Lioestheria*
malangensis MARLIÈRE, 1950, *Estheria* (*Euestheria*); Trias. (Up.); Africa (Angola) ....*Euestheria*
mangaliensis ETHERIDGE, 1892, non JONES, *Estheria* ....*Euestheria ipsviciensis*
mangaliensis GEINITZ, 1876, non JONES, *Estheria* ....*Euestheria forbesii*
mangaliensis JONES, 1863, *Estheria*; Permo-Trias. (Damuda); India ....*Euestheria*
mangaliensis by REED in LA TOUCHE, 1913, *Estheria* aff.; Devon. (?) (Wetwin sh.); Burma (Shan States) ....Estherian (?)
mangaliensis TEIXEIRA, 1947, non JONES, *Estheria*; Trias. (Up.); Africa (Angola) ....*Euestheria angolensis*
mansuyi KOBAYASHI, 1952, *Euestheria*; Trias. (Noric); Indochina (Tonkin) ....*Euestheria*
marimbensis MARLIÈRE, 1950, *Estheria* (*Echinestheria*); Trias. (Up.); Africa (Angola) ....*Echinestheria*
mathieui PRUVOST, 1927, *Estheria* (*Euestheria*); Carbon. (Up.); North China ....*Euestheria*

mawsoni JONES, 1897, *Estheria*; Cretaceous (Bahian); Brazil ....*Euestheria*
medialis KOBAYASHI and KIDO, 1945, *Estherites kyöngsanensis*; Cretaceous (Shiragi); Korea ....*Euestheria*
mellicum LUTKEVICH, 1940, *Cornia*; Perm. (Tatar.); Russia..*Cornia*
membranacea CLARKE, 1902, non PACHT, *Estheria*; ....*Asmussia clarkei*
membranacea PACHT, 1849, *Asmussia*; Devon. (Mid.); Livonia ....*Asmussia*
mendesi ALMEIDA, 1950, *Euestheria*; Rhaetic (or Lias.); Brazil ....*Euestheria*
mendocina PHILLIPI, 1887, *Estheria* (?) ....*Euestheria forbesii*
meta NOVOZHILOV, 1946, *Estheria*; Trias. (Anisic); Siberia (Chatanga) ....*Euestheria*
mezensis LUTKEVICH, 1941, *Estheria*; Perm. (Low.); Russia..*Estherites*
middendorfii CHERNYSHEV, 1930, pars, non JONES, *Estheria* ..*Euestheria middendorfii elongata*
middendorfii CHERNYSHEV, 1930, pars, non JONES, *Estheria* ..*Euestheria middendorfii jeholensis*
middendorfii COCKRELL, 1924, non JONES, *Estheria* ....*Euestheria middendorfii intermedia*
middendorfii JONES, 1862, *Estheria*; Jura. (Turga); Transbaikalia, Manchuria ....*Euestheria*
midlothianensis BOCK, 1953, *Isaura*; Trias. (Newark); N. America (Va.) ....*Euestheria*
minima PRUVOST, 1914, *Leaia tricarinata*; Carbon. (Westphalian); France ....*Leaia minima*
minoprioi RUSCONI, 1947, *Estheria* (*Pseudestheria*); Rhaeto-Lias.; Argentina (Mendoza) ....*Cornia* (?)
minuta ALBERTI in DE LA BUCHE, 1832 and GOLDFUSS in ALBERTI, 1832, *Posidonia* ....nom. nud.
minuta BOCK, 1946, non VON ZIETEN, *Estheria* ....*Euestheria* (?) *ovata*
minuta in CHAPMAN, 1914, *Estheria*; Trias.; New Zealand..*Halobia* (?)
minuta by DEFRETIN and FAUVELT, 1951, *Estheria*; Rhaeto-Lias.; Africa (Morocco) ....*Euestheria*, n. sp.
minuta by JONES, 1898, *Estheria*; Perm.; N. America (Kansas) ....*Lioestheria raaschi* (?)
minuta (?) LUTKEVICH, 1937, *Estheria* ....*Lioestheria pseudominuta*
minuta MANSUY, 1912, non VON ZIETEN, *Estheria* ....*Euestheria mansuyi*
minuta by MARLIÈRE, 1950, *Euestheria* cfr.; Perm. (Up.); Africa (Congo) ....*Euestheria* sp. nov.
minuta PICARD (1910), non VON ZIETEN, *Estheria* ....*Cyclestherioides picardi*
minuta ROGERS, 1843, *Posidonia* ....*Lioestherites ovata*
minuta VON ZIETEN, 1833, *Posidonia*; Trias. (Up.); Germany, France, Britain ....*Euestheria*
mitchelli ETHERIDGE, 1892, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Trileaia*
mitsuishii KOBAYASHI and HUZITA, 1942, *Estheria*; Cretaceous (Sungari); Manchuria ....*Estherites*
molesta RAYMOND, 1946, *Pseudestheria*; Carbon. (?); Peru ..*Cyclestherioides*

mongolensis JONES in CHERNYSHEV, 1930, *Estheria* ....(?)"*Estheria*" *mangolensis*
monocarinata LUTKEVICH, 1941, *Leaia*; Perm. (Tatar.); Russia ....*Monoleiolophus*
moutai LERICHE, 1932, *Estheriella*; Trias.; Africa (Angola)..."*Estheriella*"
multicostata EMMONS, 1857, *Estheria*; Trias. (Newark); N. America (N. Carolina, Va.) ....*Euestheria*
multilineata JONES, 1905, *Estheriella radiata*; Trias.; Malay ....*Daonella moussoni*
multinstita NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
multistriata REED, 1929, *Estheria regularis*; Perm. (Up.); Brazil ....*Estherites*
muensteriana JONES and WOODWARD, 1893, *Estheria striata*; Perm. (Rothliegend); S. Germany ....*Euestheria*
murchisoniae by IMLAY, 1941, *Estheria* aff.; Jura.; N. America (Louisiana) ....*Euestheria* sp. nov. (?)
murchisoniae JONES, 1863, *Estheria*; Jura. (Oxfordian); Scotland ....*Euestheria*
murchisoniana JONES, 1859, *Estheria*; Devon. (Mid.); Scotland, Hebrides, Shetlands ....*Asmussia*
nakazawai KOBAYASHI, 1952, *Estherites*; Trias. (Carnic); Japan ....*Estheriina*
naktongensis KOBAYASHI and KIDO, 1945, *Estherites*; Cretaceous (Naktong); Korea ....*Euestheria*
nathorsti JONES, 1883, *Estheria*; Devon. (Mid.); Spitzbergen..*Asmussia*
necta NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
nengkiangensis CHI, 1931, *Estheria*; Cretaceous (Sungari); Manchuria ....*Euestheria*
neotropica REED, 1929; *Estheria*; Perm. (Up.); Brazil ......*Estherites*
nodosa NOVOZHILOV, 1946, *Estheria*; Trias. (Anisic); Siberia (Chatange) ....*Lioestheria*
nodosocostata GIEBEL, 1857, *Posidonia*; Trias. (Buntsandstein); Germany (Thuringia) ....*Mesoleaia*
nordvikensis NOVOZHILOV, 1946, *Estheria*; Perm. (Up.); Siberia (Chatanga) ....*Lioestheria*
normalis RAYMOND, 1946, *Hemicycloleaia*; Penn.; N. America (Rhode Island) ....*Leaia*
novocastrensis MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Euestheria*
novozhilovi KOBAYASHI, nov., *Cornia* (?); Perm. (Up.); Siberia ....*Cornia* (?)
nucula FRITSCH, 1900, *Estheria*; Carbon. (Up.); Germany (Saxony) ....*Cyclestherioides*
nyasana NEWTON, 1910, *Estheriella*; Perm. (?); Africa (Nyassa) ....*Nyasestheriella*
obenaueri GUTHÖRL, 1931, *Estheria*; Perm. (Rothliegend); Germany ....*Cornia*

obliqua MITCHELL, 1927, *Estheria*; Perm. (Up.); Australia (NSW.) ....*Euestheria*

oblongata KROTOW, 1888, *Estheriella*; Perm.; Russia (Ural)..Pelecypod

oblongata MITCHELL, 1925, *Leaia*; Perm. (Belmont); Australia (NSW.) ....*Leaia*

oblongata SALINAS, 1897, *Estheria radiata*; Trias. (Carnic); Sicily ....*Halobia* or *Posidonia*?

olsoni BOCK, 1953, *Isaura*; Rhaetic (or Lias.); S. America (Venezuela) ....*Euestheria*

orientalis EICHWALD, 1865, *Estheria*; Jura. (Jehol); Transbaikalia, Manchuria ....*Euestheria middendorfii* forma *orientalis*

ortoni CHERNYSHEV, 1928, non CLARKE, *Estheria* ....*Cornia chernyshevi*

ortoni CLARKE 1900, *Estheria*; Penn. (Conemaugh); N. America (Ohio) ....*Cornia*

ovalis EMMONS, 1856, *Posidonia*; Trias.; N. America (N. Carolina) ....Estherian (?)

ovalis RAYMOND, 1946, *Orthothemos*; Cretaceous (Tsagoiana); Siberia (Seja) ....*Estherites*

ovata JONES, 1863, pars, non LEA, *Estheria* ....*Euestheria emmonsi*

ovata JONES, 1863, pars, non LEA, *Estheria* ....*Euestheria hindei*

ovata LEA, 1856, *Posidonia*; Trias. (Newark); N. America (Pa.) ....*Lioestheria*

ovata MITCHELL, 1925, *Leaia*; Perm. (Belmont); Australia (NSW.) ....*Leaia*

papillaria LUTKEVICH, 1937, *Cornia*; Perm. (Kolchugino); Siberia (Kuznetsk) ....*Cornia*

paraleidyi MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Leaia*

paralella RAYMOND, 1946, *Leaia*; Carbon. (Coal Measures); Wales ....*Leaia*

parva LEA, 1856, *Posidonia*; Trias. (Newark); N. America (Pa.) ....Estherian (?)

passani MARLIÈRE, 1950, *Estheria* (*Euestheria*); Perm. (Up.); Africa (Congo) ....*Euestheria*

paucilineata KOBAYASHI and KIDO, 1945, *Estherites kyŏngsangensis*; Cretaceous (Shiragi); Korea, (?) Manchuria ....*Euestheria*

peachi JONES, 1870, *Estheria*; Carbon. (Low.); Scotland....*Euestheria*

peipiaoensis KOBAYASHI and KUSUMI, 1953, *Estherites middendorfii*; Jurassic (Jehol), Manchuria ....*Euestheria*

pennsylvanicus WANNER, 1926, *Estheria mangaliensis*; Trias. (Newark, Shinarump?); N. America (Pa., Arizona)..*Euestheria pennsylvanicus*

petasa NOVOZHILOV, 1946, *Estheria*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*

petinensis LUTKEVICH, 1941, *Estheria*; Devon. (Up.); Russia (Don) ....*Lioestheria*

petrii ALMEIDA, 1950, *Palaeolimnadia*; Rhaetic (or Lias.); Brazil ....*Estheriina*

picardi KOBAYASHI, nov., *Cyclestherioides*; Trias. (Keuper); Germany ....*Cyclestherioides*
pincombei MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Leaia*
plicata LUTKEVICH, 1929, *Estheria*; Devon. (Mid.); Esthonia..*Euestheria*
plicifera RAYMOND, 1946, *Pseudestheria*; Perm. (Low.); N. America (Okla., Kansas) ....*Lioestheria*
pogrebovi LUTKEVICH, 1929, *Estheria*; Devon. (Mid.); Esthonia ....*Asmussia*
polita STEUSLOFF, 1894, *Bythocypris*; Cambrian (Up. ?); Germany ....*Lepiditta* (?)
portlocki JONES, 1862, *Estheria*; Perm. (Rothliegend); Ireland ....*Euestheria*
posidonomyoides CHERNYSHEV, 1930, *Estheria*; Cretaceous (Tsagoiana); Siberia (Seja) ....*Estherites*
princetonensis BOCK, 1953, *Howellites*; Trias. (Newark); N. America (N.J.) ....*Euestheria*
prisca WALCOTT, 1887, *Modiolopsis* (?); Cambrian (Low.); N. America, (N.Y.) ....*Modioloides*
proamurensis KOBAYASHI and KUSUMI, 1953, *Estherites*; Cretaceous (Kyöngsang); Manchuria ....*Cyclestherioides* (?)
pruvosti RAYMOND, 1946, *Leaia*; Carbon. (Westphalian); France, Belgium ....*Leaia raymondi*
pruvosti RAYMOND, 1946, *Palaeolimnadiopsis*; Carbon. (Westphalian); France, Belgium, Russia (Donetz) ....*Palaeolimnadiopsis*
pruvosti REED, 1929, *Leaia*; Perm. (Up.); Brazil ....*Leaia*
pseudominuta KOBAYASHI, nov., *Lioestheria*; Trias. (Maltsévo); Siberia (Kuznetsk) ....*Lioestheria*
pulex CLARKE, 1882, *Estheria*; Devon. (Mid.); N. America (N.Y.) ....*Rhabdostichus*
punctatella JONES, 1865, *Estheria*; Carbon.; Scotland ......*Posidonomya* (?)
quadrata MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Leaia*
quadricarinata LUTKEVICH, 1929, *Praeleaia*; Devon. (Mid.); Esthonia ....*Praeleaia*
quadriradiata MITCHELL, 1925, *Leaia*; Perm. (Up.); Australia (NSW.) ....*Quadrileaia*
quinquecarinata LUTKEVICH, 1929, *Praeleaia*; Devon. (Mid.); Esthonia ....*Praeleaia*
raaschi RAYMOND, 1946, *Lioestheria*; Perm. (Low.); N. America (Okla.) ....*Lioestheria*
radiata SALINAS, 1897, *Estheria*; Trias. (Carnic); Sicily....*Halobia* (?)
rampoensis KOBAYASHI, 1950, *Estherites*; Trias. (Daido); Korea, (?) Manchuria ....*Cyclestherioides*
raricostata CHERNYSHEV, 1926, *Estheriella*; Carbon. (Westphalian); Russia (Donetz) ....*Anomalonema* (?)
raymondi KOBAYASHI, 1952, *Leaia*; Carbon. (Westphalian); France ....*Leaia*

rectangula YOKOYAMA, 1894, *Estheria*; Cretaceous (Low.); Japan ....*Pseudoleaia*
reflexa RAYMOND, 1946, *Leaia*; Perm. (Low.); N. America (Okla.) ....*Leaia*
regio-borisi PRANTL, 1939, *Leaia*; Carbon.; Burgaria........*Leaia* (aff. *minuta*.)
regio-ferdinandi PRANTL, 1939, *Leaia*; Carbon.; Burgaria ..*Leaia* (aff. *minuta*)
regoi ALMEIDA, 1950, *Acantholeaia*; Perm.; Brazil ....*Acantholeaia*
regularis REED, 1929, *Estheria*; Perm. (Up.); Brazil........*Estherites*
reinachii JONES and WOODWARD, 1893, *Estheria*; Perm. (Rothliegend); Germany ....*Euestheria*
reticulata CHERNYSHEV, 1930, *Estheria*; Jura. (Karabon); Siberia ....*Euestheria*
reticulata KOBAYASHI, 1951, non CHERNYSHEV, *Estherites* aff. ....*Euestheria kidoi*
reumauxi PRUVOST, 1911, *Estheriella*; Carbon. (Westphalian); France, Russia (Donetz) ....*Anomalonema*
rhenana HARTUNG, 1939, *Leaia*; Carbon. (Namur.), Germany ....*Leaia*
rimosa GOLDENBERG, 1877, *Estheria*; Carbon. (Stephanian); Germany (Saarbrücken) ....*Euestheria*
rotunda LUTKEVICH, 1941, *Estheria*; Perm. (Tatar.); Russia ....*Lioestheria*
rotundula LUTKEVICH, 1937, *Estheria*; Devon. (Up.); Russia (Timan) ....*Asmussia*
rugosa GÜMBEL, 1864, *Estheria*; Perm.; Germany (Thuringia) ....Estherian, gen. indt.
rugosa RAYMOND, 1946, *Pseudestheria*; Perm. (Low.); N. America (Okla.) ....*Lioestheria*
saitoi KOBAYASHI and KUSUMI, 1953, *Estherites*; Cretaceous (Kyöngsang); Manchuria ....*Cyclestherioides*
salteriana JONES, 1862, *Leaia leidyi*; Carbon. (Low.); Scotland ....*Leaia salteriana*
schopeni SALINAS, 1897, *Estheria*; Trias. (Carnic); Sicily....*Posidonia* (?)
septentrionalis KOBAYASHI and HUZITA, 1942, *Estheria*; Cretaceous (Sungari); Manchuria ....*Euestheria*
shimamurai KOBAYASHI, 1950, *Estherites*; Trias. (Carnic?); Korea, (?) Manchuria ....*Euestheria*
sibericensis RAYMOND, 1946, *Limnadopsis*; Cretaceous (Tsagoiana); Siberia (Seja) ....*Palaeolimnadiopsis*
sigillata MATTHEW, 1894, *Lepiditta*; Cambrian (Low.); N. America (New Brunswick) ....*Lepiditta* (?)
silurca MATTHEW, 1910, *Leaia*; Devon. or Permo-Carbon. (Little River); Canada (New Brunswick) ....*Leaia*
simoni PRUVOST, 1911, *Estheria*; Carbon. (Westphalian); England, France, Russia (Donetz), Morocco ....*Lioestheria* (?)
sinensis CHI, 1931., pars, *Estheria middendorfii*; Jura. (Up.) Cretaceous (Low.); China ....*Euestheria*
sinensis CHI, 1931, pars, *Estheria middendorfii*, ...*Estherites mitsuishii*

sinkiangensis CHI, 1931, *Estheria*; Jura.; China (Sinkiang)..*Euestheria*
sinuata LUTKEVICH, 1929, *Estheria*; Devon. (Mid.); Esthonia..*Asmussia*
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stockmansi MAILLIEUX, 1939, *Estheria* (*Euestheria*); Devon. (Low.); Belgium ....*Euestheria*
stowiana JONES and WOODWARD, 1894, *Estheria* ....*Estherites draperi*
striata GOLDFUSS and MÜNSTER, 1840, *Sanguinolaria*; Carbon. (Dinantian, Westphalian); Germany, Belgium, France, Scotland ....*Lioestheria*
strictocostata NOVOZHILOV, 1946, *Polygrapta*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*
striolatissima RUSCONI, 1948, *Euestheria*; Trias. (Rhaetic); Argentina (Mendoza) ....*Euestheria*
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subconcentrica KROTOW, 1888, *Estheria*; Perm. (Up.); Russia (W. Ural.) ....Pelecypod
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subquadrata SOWERBY, 1836, *Cyclas*; Jura. (Purbeckian), Cretaceous (Wealden); England ....*Euestheria*
subulata REED, 1929, *Estheria*; Permo-Trias.; Brazil ......*Palaeolimnadiopsis*
sulcata KOBAYASHI, nov., *Paraleaia*; Perm. (Up.); Australia (NSW.) ....*Trileaia*
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tanii KOBAYASHI, 1951, *Estherites*; Rhaeto-Lias. (?); Korea..*Asmussia*
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tenella BRONN, 1850, *Posidomya*; Perm. (Low.); Germany ..*Asmussia*

tenuipectoralis JONES, 1883, *Estheria striata*; Carbon. (Low.); Russia (Ural) ....*Asmussia*

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tigjanensis NOVOZHILOV, 1946, *Diaplexa*; Trias. (Anisic); Siberia (Chatanga) ....*Lioestheria*

timanica LUTKEVICH, 1941, *Estheria*; Devon. (Up.); Russia (Timan) ....*Asmussia* (?)

toricata NOVOZHILOV, 1946, *Estheria*; Perm. (Up.); Siberia (Chatanga) ....*Euestheria*

transbaikalica CHERNYSHEV, 1930, *Estheria*; Jura. (Karabon); Siberia (Transbaikalia) ....*Euestheria*

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trapezoidalis NETSCHAJEW, 1894, *Estheria*; Perm. (Tatar.); Russia (Dwina), Siberia (Chatanga) ....*Lioestheria*

triassiana LUTKEVICH, 1929, *Praeleaia*; Trias. (Maltsévo); Siberia (Kuznetsk) ....*Metaleaia*

tricarinata MEEK and WORTHEN, 1868, *Leaia*; Penn. (Carbondale ?); N. America (Ill., Ind.) ....*Leaia*

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tuberculata NOVOZHILOV, 1946, *Diaphora*; Trias. (Anisic); Siberia (Chatanga) ....*Lioestheria*

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unicostata REED, 1929, *Leaia*; Perm. (Up.); Brazil ....*Monoleiolophus*

unicostatus RAYMOND, 1946, non REED, *Monoleiolophus*........*Monoleiolophus conemaughensis*

venekiensis LUTKEVICH, 1938, *Estheria*; Trias. (Low.); Siberia (Tungusska) ....*Estherites* (?)

ventriculita NOVOZHILOV, 1946, *Estheria*; Perm. (Up.); Siberia (Chatanga) ....*Asmussia*

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weissi FRITSCH, 1900, *Leaia*; Carbon. (Stephanian); Germany (Saxony) ....*Paraleaia* (?)
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wellerorum RAYMOND, 1946, *Hemicycloleaia*; Penn.; N. America (Ill.) ....*Leaia*
wengensis GIEBEL, 1857, non WISSMANN, 1841, *Posidonia* ....*Estheriella costata*
wettinensis FRITSCH, 1900, non LASPEYRES, *Leaia* ....*Paraleaia fritschi*
wettinensis LASPEYRES, 1870, *Leaia*; Carbon. (Stephanian); Germany (Saxony) ....*Leaia*
wianamattensis MITCHELL, 1927, *Estheria*; Trias.; Australia (NSW.) ....*Estherites*
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winterpockensis BOCK, 1953, *Howellites*; Trias. (Newark); N. America (Va.) ....*Euestheria*
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POSTSCRIPTS

1. *Palaeestheria* sp. (RENNIE, 1934) found in the Witteberg series of the Cape system in South Africa at Port Alfred in association with *Haplostigma irregulare* is an oblong cycladiform dilating posteriorly. No sculpture is seen in the interspace. Because a nuclear node is said to exist at the umbo which is terminal on the dorsal margin, it may be a *Cornia* and if so, this species is the oldest of the genus, because the Witteberg flora is Devonian and perhaps Middle Devonian and the Witteberg series lies conformably beneath the Karroo system.

2. *Palaeestheria lebombensis* RENNIE was procured from the Lebombo volcanic formation at Namahacha, west of Lourenço Marques in the colony of Moçambique together with *Otozamites* cfr. *bechei* (BRONGNIART), *Pagiophyllum* (?) sp., *Unio andradei* RENNIE and *Viviparus* (?) sp. Liassic was suggested for the age of the formation by A.L. DE TOIT (the volcanic belt of Lebombo — a region of tension. *Trans. Roy. S. Afr. Vol. 18*, 1929).

The holotype of the Estherian species is 6.5 mm. high and 4.5 mm. long; its hinge line 5 mm. long. The Estherian has an ovate-oblong carapace with subterminal umbones; numerous narrow raised concentric ridges, about 10 per mm. near the ventral margin, equidistant; their interspaces are relatively broad, concave and crossed by radial lirae. Because the interspace is ornamented with these radial lirae as shown in the text-figure (RENNIE, 1939, p. 21), this species is referred to *Euestheria*.

3. Prof. B.F. HOWELL of the Princeton University kindly informed me of the fact that "I once had a chemist test a specimen of *Fordilla* to learn whether it was phosphatic. He could find no trace of phosphorus in it." (Personal communication, Nov. 23, 1953).

4. "There is considerable possibility that the Ribeiridae should be separated from Notostraca and placed in an independent and new order", (KOBAYASHI, 1933, p. 313). A note is given here for Ribeirida proposed on page 31.

Order Ribeirida KOBAYASHI, nov.

Diagnosis: — Carapace calcareous, univalved, but folded down like bivalves, generally gapping on fore- and rear-sides like slits and in some genera winged on one or two sides; posterior side sometimes distinctly flattened and a well defined opening found on flattening; carina in addition to a groove extending from umbo in certain genera. Surface smooth, or ornamented by radial or concentric ribs or striae. Internally one or two clavicles always exist, but no teeth, adductor, scars, pallial line or ligaments.

Remarks: — Nothing is known of the soft part. Like in *Apus* the carapace is univalved, but folded down ventrally and not truncated on the rear side. This may be an extinct group of Crustacea rather than Mollusca. Its genetical relation to *Heraultia* and other middle and early Cambrian genera is still in question.

This order comprises 14 genera which can be classified into the Eopteridae MILLER (Ribeiridae KOBAYASHI) with a single clavicle and the Ischyriniidae KOBAYASHI, nov. (Ischyrininae KOBAYASHI) with double clavicles.

Distribution: — Cosmopolitan (KOBAYASHI, T. 1936); appeared in late Cambrian in Eastern Asia and developed in Ordovician when the Conchostraca declined,

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